

Stenotopic *Hormurus* Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896

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Stenotopic *Hormurus* Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896. - Three new species from the semi-arid ecosystems of Queensland, Australia, are described in the present contribution: *Hormurus ischnoryctes* n. spec., *Hormurus macrochela* n. spec., *Hormurus ochyroscapter* n. spec. Additionally, the discovery of the first female specimens of *Hormurus longimanus* (Locket, 1995) from the Northern Territory of Australia, as well as additional diagnostic characters and locality records for this species, warranted its redescription. *Hormurus longimanus* (Locket, 1995) is reinstated as the valid name for this species and the replacement name, *Liocheles extensus* Locket, 1997 placed in synonymy. Unlike most species of *Hormurus* and of the closely related genera, *Hormiops* Fage, 1933 and *Liocheles* Sundevall, 1883, which inhabit humid tropical ecosystems (evergreen forests), the four Australian species treated here inhabit seasonally dry (monsoon) habitats, and two of these (*H. ischnoryctes* and *H. ochyroscapter*) are the first fossorial hormurids to be recorded in Australia, and the first fossorial species of *Hormurus* to be described. The four species treated here appear to be relicts of an old hygrophilous lineage that sustained a major adaptive radiation during the late Tertiary aridification of the continent. Endemism and conservation issues concerning these phylogenetically valuable species are discussed in the context of high sensitivity to habitat disturbance and high risk of extinction of stenotopic species.

Keywords: *ischnoryctes* - *longimanus* - *macrochela* - *ochyroscapter* - taxonomy - ecology - Queensland - Northern Territory.

INTRODUCTION

The hormurid scorpion genus *Liocheles* Sundevall, 1883 was recently redefined, and two genera previously synonymized with it, i.e. *Hormiops* Fage, 1933 and *Hormurus* Thorell, 1876, were resurrected on the basis of a phylogenetic analysis (Monod, 2011; Monod & Prendini, in preparation). *Hormurus* is a conspicuous element of the Australasian scorpion fauna, with eight species currently recognized, all occurring east of Huxley's (1868) line. An ongoing taxonomic revision of the three genera has uncovered an unsuspected diversity. Three new species, *Hormurus ischnoryctes* n. spec., *Hormurus macrochela* n. spec., and *Hormurus ochyroscapter* n. spec., from semi-arid ecosystems of Queensland, Australia, are described in the present contribution, raising the number of accepted species in the genus to eleven. A fourth species, *Hormurus longimanus* Locket, 1995 from the Northern Territory, is redescribed following the discovery of the first female specimens, and additional diagnostic characters and locality records are provided.

These four Australian species are remarkable in several respects: all apparently have very restricted distributional ranges, all occur in much drier habitats than most other species of *Hormurus* and of the closely related *Hormiops* and *Liocheles*, which inhabit humid tropical ecosystems (evergreen forests) throughout the Indo-Pacific region, and all have developed unique morphological and/or behavioural characters in response to their habitats. *Hormurus longimanus* and *H. macrochela* are strictly lithophilous, inhabiting the narrow cracks and crevices of weathered rock outcrops, and are characterized by extreme sexual dimorphism in the length and shape of the pedipalps. In contrast, *H. ischnoryctes* and *H. ochyroscapter* are short, robust species adapted for burrowing in the ground, with modest sexual dimorphism in the pedipalps. These two species are the first fossorial hormurids recorded from Australia, and the first fossorial species of *Hormurus* to be described. Among the three genera mentioned above, burrowing was previously reported only in the pelophilous species *Liocheles nigripes* (Pocock, 1897) (Fig. 1) from the woodlands and forests of India (Tilak, 1970). The rarity of fossorial *Hormurus* species might be attributed to their restricted distributions, which may, in turn, be related to their stenotopic substratum requirements, as observed in other fossorial hormurids (Prendini, 2001).

The four *Hormurus* species treated in the present paper appear to have evolved from more generalist lithophilous ancestors in response to the late Tertiary aridification of Australia and the concomitant contraction and fragmentation of rainforests that covered the continent throughout the Paleogene (Monod, 2011; Monod, Harvey & Prendini, in preparation). These scorpions probably represent relicts of a formerly widespread lineage that persisted in rocky habitats in forest refugia and along river systems, and are thus important for reconstructing the historical biogeography of *Hormurus* on the Australian continent.

These species of *Hormurus* are also at a greater risk of extinction than others owing to their restricted habitat requirements, limited vagility, and small isolated populations. As emphasized by Prendini (2001), substratum specialists (stenotopes) usually have more restricted distributions than substratum generalists (eurytopes), and are more vulnerable to habitat perturbation because of their lower ecological plasticity. In the monsoon ecosystems of tropical northern Australia, the small size and fragmen-



FIG. 1

Liocheles nigripes (Pocock, 1897), male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

tation of habitats suitable for *Hormurus* species increases the vulnerability of each population to environmental stochasticity. The survival of localised populations depends entirely on the protection of their habitat islands. *Hormurus longimanus* is restricted to small patches of monsoon forests scattered along the western escarpment of the Arnhem Land Plateau, a habitat that depends entirely on rainfall and the water storage capacity of rock aquifers for its persistence. Similarly, the habitat of *H. ischnoryctes* endures the dry season by the gradual discharge of ground water stored in a nearby rock formation. The mining industry, livestock, feral animals and fire represent significant threats to these fragile habitats and consequently also to the survival of their autochthonous biota, including scorpions.

MATERIAL AND METHODS

FIELDWORK: Most specimens examined were collected during field surveys in the Northern Territory and Queensland, Australia. Scorpions were collected during the day by inspecting rock crevices and exfoliations, or by excavating burrows and at night with ultraviolet (UV) light (Stahnke, 1972) using a portable Maglite lamp equipped with a UV LED retrofit (Xenopus Electronix, Austin, TX, U.S.A.).

GEOREFERENCING: Exact geographical coordinates of collecting localities were recorded using a portable GPS device (Garmin E-trek Summit). Only coarse data, rounded to the nearest 10 seconds, are provided in the present publication following the recommendations of Chapman & Grafton (2008). Geographical coordinates for records without GPS data were traced by reference to gazetteers and the GEONet Names Server (<http://earth-info.nga.mil/gns/html/index.html>) and are given between brackets.

MAPPING: Distribution maps were produced using ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, CA, USA) by superimposing point locality records on a SRTM 90 m (3 arc-second) digital elevation model (Jarvis *et al.*, 2008) and a SRTM 1 km (30 arc-second) global bathymetry dataset (Becker *et al.*, 2009).

ABBREVIATIONS: Collections containing material examined in the present study are abbreviated as follows: AM, Australian Museum (Sydney, New South Wales, Australia); AMNH, American Museum of Natural History (New York, U.S.A.), including tissues samples stored in the Ambrose Monell Cryocollection (AMCC); CUNY, City University of New York (New York, USA); EPA, Environmental Protection Agency (Queensland, Australia); ESV, Erich S. Volschenk private collection (Perth, Western Australia); MHNG, Muséum d'histoire naturelle (Geneva, Switzerland); MNHN, Muséum National d'Histoire Naturelle (Paris, France); NHML, Natural History Museum (London, United Kingdom); NTM, Northern Territory Museum of Arts and Sciences (Darwin, Northern Territory, Australia); QM, Queensland Museum (Brisbane, Queensland, Australia); WAM, Western Australian Museum (Perth, Western Australia).

MORPHOLOGICAL TERMINOLOGY AND MENSURATION: Morphological terminology follows Vachon (1956, 1963) for cheliceral dentition, Stahnke (1970) for pedipalp segmentation, Vachon (1974) for trichobothrial patterns, Couzijn (1976) for leg segmentation, Lamoral (1979), modified by Monod & Volschenk (2004), for

hemispermatochore morphology, and Prendini (2000) for carapace sulci and sutures, and pedipalp and metasomal carinae. The postocular carapace margin refers to a strip of the lateral margin immediately posterior to the lateral ocelli (see pcm in Fig. 4). Measurements follow Stahnke (1970) and were recorded in mm using an ocular micrometer or digital calipers.

EXAMINATION: Specimens were examined with a NIKON SMZ1500 stereomicroscope at the AMNH, and with ZEISS Stemi SV8 and SV11 stereomicroscopes at the MNHG. Ultrasonic treatment (sonication) was used to remove adhering mud and soil particles, which obscure fine details, from the tegument of specimens (Nowak *et al.*, 2008). Specimens were immersed in soapy water in a digital ultrasonic cleaner for 15-90 seconds, and the procedure repeated until satisfactorily cleaned. More, shorter rounds of sonication were conducted on smaller and older specimens to avoid damage. Specimens were rinsed with distilled water after sonication.

DISSECTION: Hemispermatochores were dissected from adult male specimens using microsurgical scissors and forceps. Paraxial organ tissue was removed manually with forceps or chemically with diluted (50%) Proteinase K (Qiagen, Venlo, The Netherlands). Hemispermatochores were placed in the Proteinase K solution in an oven at 45-50°C for 15 minutes to an hour, depending on size and degree of sclerotization. After soft tissues were sufficiently digested, the hemispermatochores were removed from the solution and rinsed with distilled water.

PHOTOGRAPHS AND ILLUSTRATIONS: High resolution images of diagnostic characters were taken under long-wave UV and visible light with a Microoptics ML 1000 digital imaging system at the AMNH and a custom-built system at the MHNG. CombineZM and CombineZP (Hadley, 2005, 2009) were used to fuse images taken at different focal planes into a single image with greater depth of field. Line drawings of hemispermatochores were produced using a camera lucida mounted on the stereomicroscopes. Pencil sketches were subsequently inked and scanned for further processing and editing. Illustrations and photographs were edited (background removal and contrast adjustment) in Adobe Photoshop CS5 and plates prepared with Adobe Illustrator CS5 (both from Adobe Systems, San Jose, CA, U.S.A.). Colour drawings were produced as digital media based on scientific illustrations and photographs of live specimens to accurately represent the colours present in life.

UV FLUORESCENCE IMAGING: The macrosculpture of the tegument surface of scorpions is an important source of diagnostic and phylogenetic characters but may be difficult to examine and image under visible light as it is often obscured by pigmentation beneath the cuticle or by reflection from the shiny parts of the cuticle. UV fluorescence imaging, exploiting the fluorescence property of the epicuticle when exposed to long wave UV radiation (Lawrence, 1954; Pavan, 1954a, b, c; Pavan & Vachon, 1954; Stahnke, 1972; Stachel *et al.*, 1999), overcomes these problems and, when combined with focus-stacking, allows the production of scanning electron microscope (SEM)-quality images without the elaborate and destructive preparations required for the latter (Volschenk, 2002, 2005). The technique is now widely used in scorpion systematics (Prendini, 2003a, b, 2004, 2005a, 2006; Prendini *et al.*, 2003, 2006; Ojanguran-Affilastro *et al.*, 2007, 2009; Vignoli & Prendini, 2008, 2009; Navidpour &

Lowe, 2009). Its primary shortcoming is the need for high sensitivity settings due to the limited amount of light provided by UV flashes. However, recent technological advances in digital SLR cameras have considerably improved the resolution of images taken under low light conditions.

SCANNING ELECTRON MICROSCOPY (SEM): SEM was used to explore the fine structure of the capsular region of the hemispermaphore, using the Microscopy and Imaging Facility at the AMNH. Hemispermaphores were dehydrated in a graded alcohol series, critical point dried in a Baltec 030 critical point dryer, mounted on standard aluminium stubs (diameter 12 mm, height 7 mm; Electron Microscopy Sciences), and sputter-coated with gold/palladium in a Denton Vacuum Desktop II. Samples were examined with a Hitachi S4700 field emission SEM.

Family **HORMURIDAE** Laurie, 1896

Genus *Hormurus* Thorell, 1876

Hormurus longimanus (Locket, 1995)

Figs 2-11, Table 1

Liocheles longimanus Locket, 1995: 191-198, figs 1-14 [junior secondary homonym of *Liocheles australasiae longimanus* (Werner, 1939), here reinstated (see Remarks)]. – Kovařík, 1998: 134.

Liocheles extensa Locket, 1997: 331 (replacement name for *L. longimanus* Locket, 1995; incorrect original spelling). – Volschenk *et al.*, 2001: 162. – Monod, 2000: 86-90, pl. 31, map 10 **syn. n.**

Liocheles waigiensis (Gervais, 1843). – Volschenk *et al.*, 2001: 162 (misidentification, part).

Liocheles extensus. – Fet, 2000 (mandatory change of ending): 397. – Monod & Volschenk, 2004: 675, 686 (part).

HOLOTYPE: NTM A000196; ♂; Australia, Northern Territory, Arnhem Land, Oenpelli area [13°19'36"S, 133°03'23"E]; 21-22.VII.1992; A. Wells & J. Webber.

PARATYPE: NTM A000197; 1 ♂; Australia, Northern Territory, Kakadu National Park, 13°20'S, 139°40'E; 20.II.1994; under decaying bark in monsoon vine forest, G. Wallis.

OTHER MATERIAL: QM-S23252; 1 ♀, 1 imm.; Australia, Northern Territory, Gorge NE of Mount Gilruth [13°03'S, 133°05'E]; 10-13.VII.1979; rainforest, G. B. Monteith & D. J. Cook. – WAM 98/1852-5; 4 imm.; Kakadu National Park, Jim Jim Falls, 13°20'S, 132°50'E; 31.V.1992; under rocks, M. S. Harvey & J. M. Waldock. – WAM T129144; 1 ♂, 4 ♀, 2 imm.; idem; 21-22.VIII.2009; 64-129 m, monsoon forest, in rock crevices, G. Brown & L. Monod. – MHNG, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMNH, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMCC LP 10318; ♂ [1 leg], 1 imm.; same data as previous record. – WAM T129145; 1 ♀; Kakadu National Park, Koolpin Creek 13°30'S, 132°30'E; 24.VIII.2009; 107 m, vine thicket beside creek, in rock crevices, G. Brown & L. Monod. – MHNG, without registration number; 1 ♀; same data as previous record. – AMNH, without registration number; 1 ♀; same data as previous record. – AMCC LP 10317; ♀ [1 leg], ♀; same data as previous record. – WAM T129146; 2 ♂, 3 ♀, 2 imm.; Kakadu National Park, Maguk, 13°20'S, 132°30'E; 23.VIII.2009; 98 m, monsoon forest beside pools, in rock crevices, G. Brown & L. Monod. – MHNG, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMNH, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMCC LP 10314; ♀ [2 legs]; same data as previous record.

REMARKS: *Liocheles extensa* was introduced by Locket (1997) as a replacement name for *Liocheles longimanus* Locket 1995 to remove the secondary homonymy with *Liocheles australasiae longimanus* (Werner, 1939). *Liocheles longimanus* Locket, 1995, now transferred to the genus *Hormurus*, is no longer a junior secondary homonym of *Liocheles longimanus* (Werner, 1939) (which remains in the genus *Liocheles*),

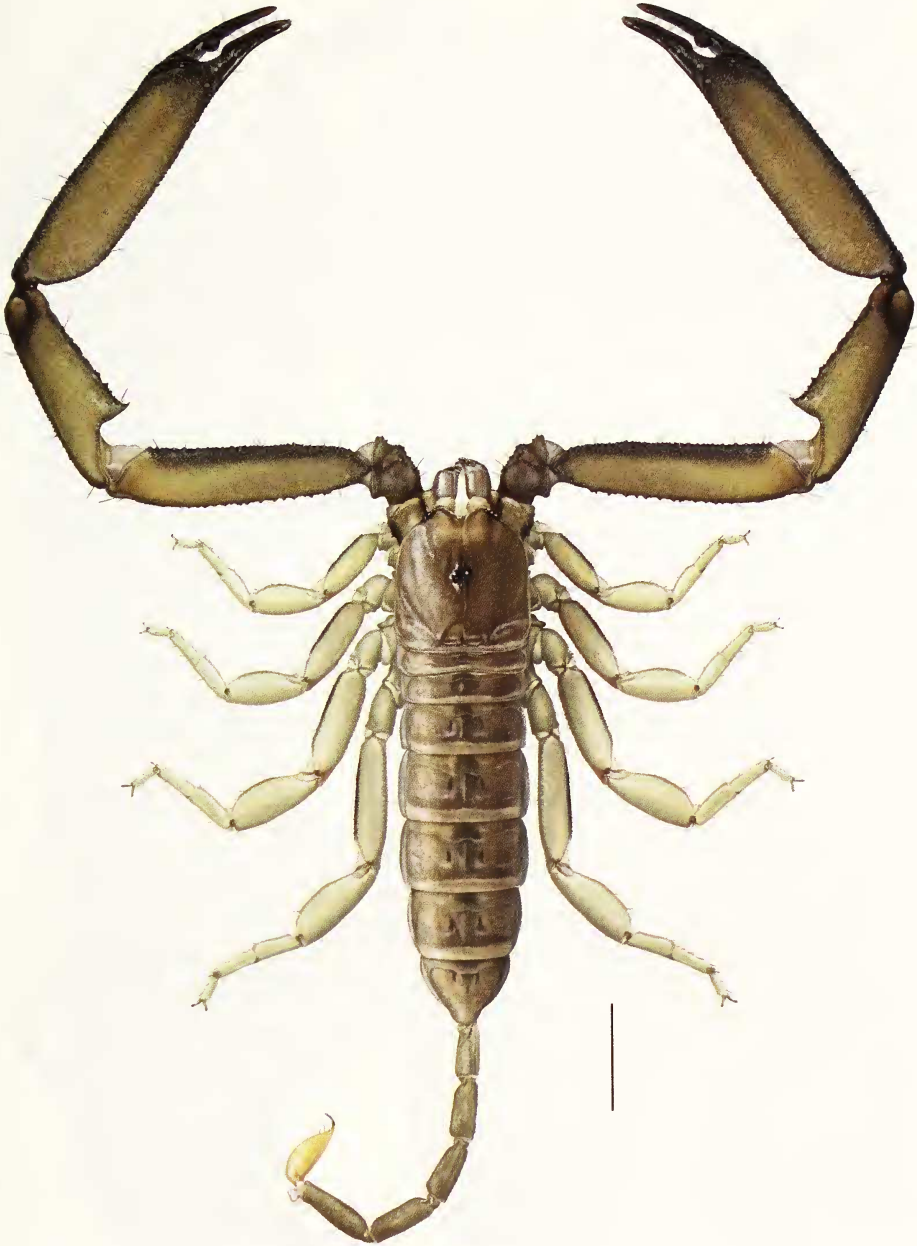


FIG. 2

Hormurus longimanus (Locket, 1995), male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.



FIG. 3

Hormurus longimanus (Locket, 1995), habitus, dorsal (A, B) and ventral (C, D) aspect. (A, C) Male (MNHG). (B, D) Female (MNHG). Scale, 5 mm.

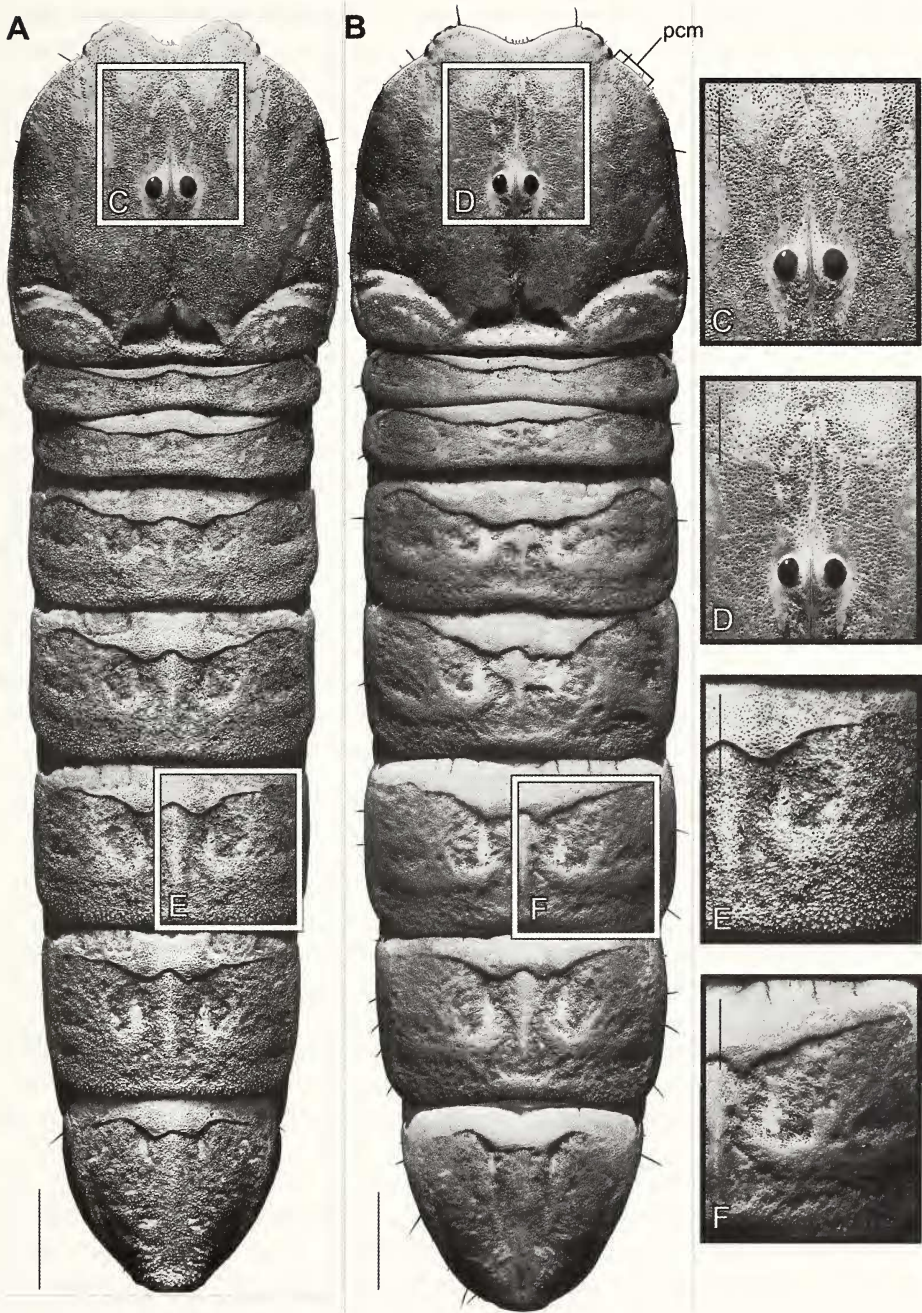


FIG. 4

Hormurus longimanus (Locket, 1995), carapace and mesosomal tergites, illustrating ornamentation and macrosculpture of cuticle (A, B), with detailed view of carapace (C, D) and tergite V (E, F), dorsal aspect. (A, C, E) Male (MNHG). (B, D, F) Female (MNHG). Abbreviation: pcm (postocular carapace margin). Scale, 2 mm (A, B), 1 mm (C-F).

and is thus reinstated in accordance with article 59.4 of the International Code of Zoological Nomenclature (ICZN, 1999). *Liocheles extensus* Locket, 1997 thus becomes a junior objective synonym of *Hormurus longimanus* (Locket, 1995).

DIAGNOSIS: *Hormurus longimanus* differs from other Australian species of the genus as follows. Sexual dimorphism of the pedipalps is more pronounced in *H. longimanus* than in other species except *H. macrochela*. The base colouration of the cuticle (tan to light brown) is much paler in *H. longimanus* than in other species except *H. ochyroscapter*. In the adult male of *H. longimanus*, the suprabasal lobe of the pedipalp chela movable finger is conical (at least as high as wide), unlike in other species in which it is rounded (wider than high); when the fingers are closed, a distinct proximal gap is evident between this lobe and the corresponding notch on the chela fixed finger in *H. longimanus*, whereas in other species the lobe and notch fit contiguously, without a proximal gap; the suprabasal lobe overlaps the retrolateral surface of the fixed finger distal to the gap in *H. longimanus*, whereas in other species there is no overlap; and the basal lobe of the chela fixed finger is extremely reduced in *H. longimanus*, compared to the well developed conical lobe observed in other species. Additionally, the dorsal surface of the chela manus is finely and densely granular in *H. longimanus*, whereas in other species the granulation is coarser. The posterior spiniform granules of the dorso-submedian carinae of metasomal segments III and IV are noticeably larger than the preceding granules in *H. longimanus*, unlike other species in which they are similar. The ventro-submedian carinae of metasomal segments I and II possess two or three pairs of well developed subposterior spiniform granules and 4-6 (I) or 4-5 (II) pairs of small median spiniform granules in *H. longimanus*, compared to other species in which the carinae possess two or three pairs of small subposterior granules and one or two pairs of small median granules. The ventrolateral carinae of metasomal segment II possess one pair of subposterior spiniform granules in *H. longimanus*, compared to other species in which the carinae possess no distinct granules.

DESCRIPTION OF ADULT MALE: *Colouration:* Dorsal surface of chelicera manus pale brown; fingers slightly darker (Fig. 2). Carapace pale brown. Pedipalps yellow to pale brown; carinae and fingers reddish brown to black. Legs pale yellow. Tergites pale brown, slightly paler than carapace; posterior margin with yellow stripe. Coxapophyses, sternum, genital operculum, pectines and sternites pale yellow. Metasoma pale brown. Telson yellow; aculeus reddish black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma and metasoma finely punctate.

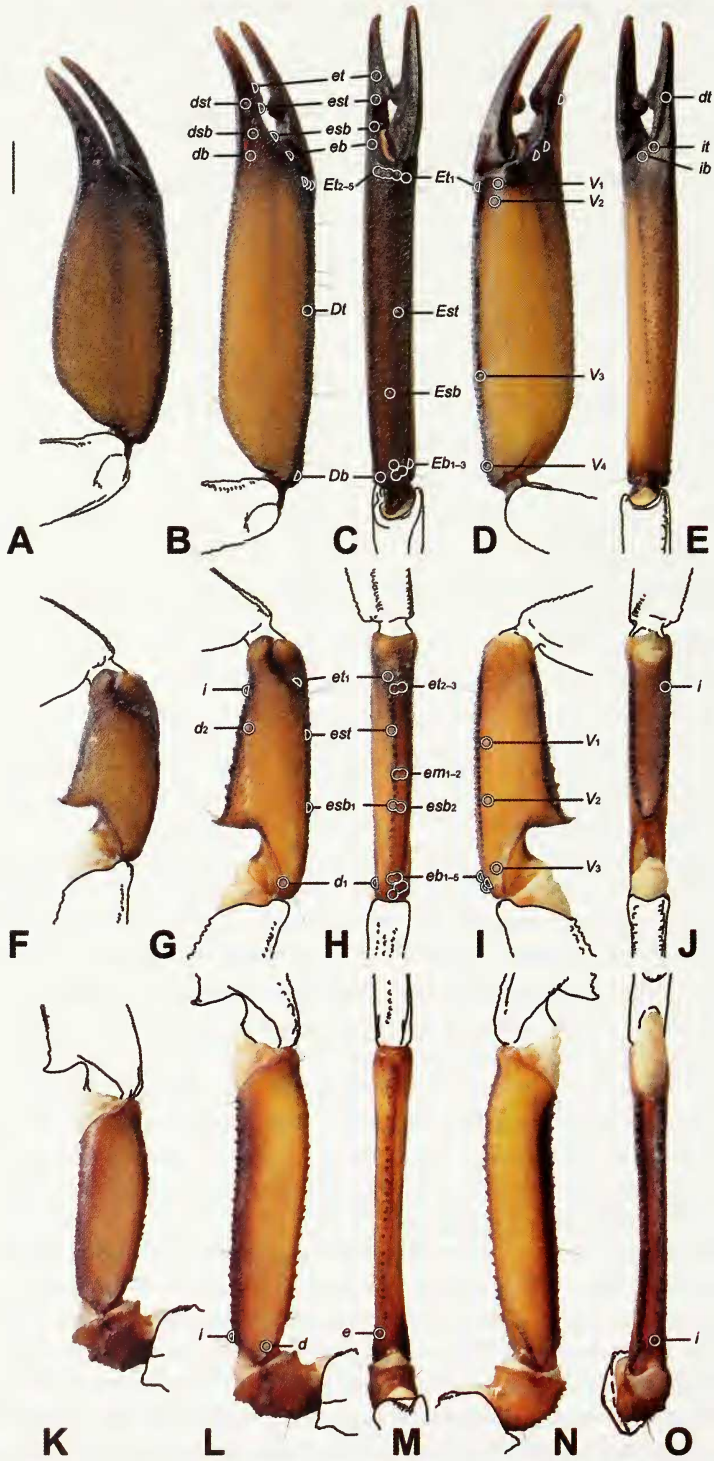
Carapace: Anterior margin with shallow median notch (Fig. 4A). Anterior furcated suture and sulci distinct. Median ocular tubercle situated anteromedially, slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated from each other by at least half the diameter of a median ocellus. Three pairs of lateral ocelli, all equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces finely and densely granular (creating a matte appearance) except anteromedially, with frontal lobes smooth, fine granulation restricted to surfaces adjacent to anterior furcated sulcus and median longitudinal sulcus (Fig. 4C).

TABLE 1. *Hormurus longimanus* (Locket, 1995), measurements (in mm) of adult males and females.

Sex	♂	♂	♂	♀	♀	♀
Repository	MHNG	AMNH	AMNH	QM-S 23252	WAM	AMNH
Locality	Jim Jim Falls	Maguk	Jim Jim Falls	Mt Gilruth	Jim Jim Falls	Koolpin Creek
Total length	44	36	38	48	41	36
Carapace, length	6.0	5.8	5.8	6.9	5.9	5.7
Carapace, anterior width	3.7	3.5	3.3	4.3	3.6	3.3
Carapace, posterior width	6.6	6.3	5.9	7.1	6.6	6.1
Chela, length	18.3	16.7	16.0	16.1	13.9	13.7
Chela manus, width	3.6	3.8	3.4	4.5	4.3	4.4
Chela manus, height	1.7	1.6	1.5	1.7	1.7	1.6
Chela movable finger, length	7.1	6.7	6.3	6.8	6.0	5.8
Patella, length	10.4	9.3	8.8	8.1	7.2	6.8
Patella, width	3.0	2.9	2.8	3.4	3.2	3.1
Femur, length	12.0	10.8	10.8	9.3	8.2	8.0
Femur, width	2.7	2.8	2.5	2.9	2.8	2.5
Metasomal segment I, length	2.7	2.3	2.5	2.9	2.5	2.6
Metasomal segment I, width	1.2	1.1	1.1	1.3	1.2	1.2
Metasomal segment V, length	4.0	3.8	3.6	3.9	3.9	3.7
Metasomal segment V, width	1.1	1.0	0.9	1.0	1.0	0.9
Metasomal segment V, height	1.1	1.0	1.0	1.1	1.1	1.0
Telson vesicle, width	1.0	1.0	1.0	1.1	1.0	0.8
Telson vesicle, height	1.2	1.0	1.0	1.3	1.1	1.0

Chelicerae: Median and basal teeth of fixed finger fused into a bicusp. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: Pedipalp segments extremely long and slender (Figs 2, 3A, C, 5B-E, G-J, L-O, 6A), with femur length twice carapace length (Tab. 1). Chela almost asetose. *Chela fingers*: Dentate margins of fixed and movable fingers linear (without lobe and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe reduced; suprabasal notch distinct and deep (Fig. 6A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, conical (as high as or higher than wide), gently rounded dorsally, lacking a sharp conical tooth, and overlapping retrolateral surface of fixed finger (in anterior part of notch); distinct proximal gap present between suprabasal lobe and corresponding suprabasal notch of fixed finger when fingers closed. *Pedipalp carinae*: Femur (Fig. 5L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal carina obsolete, without granules; internomedian ventral carina vestigial, comprising two large spiniform granules situated proximally and medially on segment; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 5G-J): Prolateral process strongly developed, forming prominent median spine; internodorsal and dorsomedian carinae distinct; dorsoexternal carina obsolete; externomedian carina granular; ventroexternal



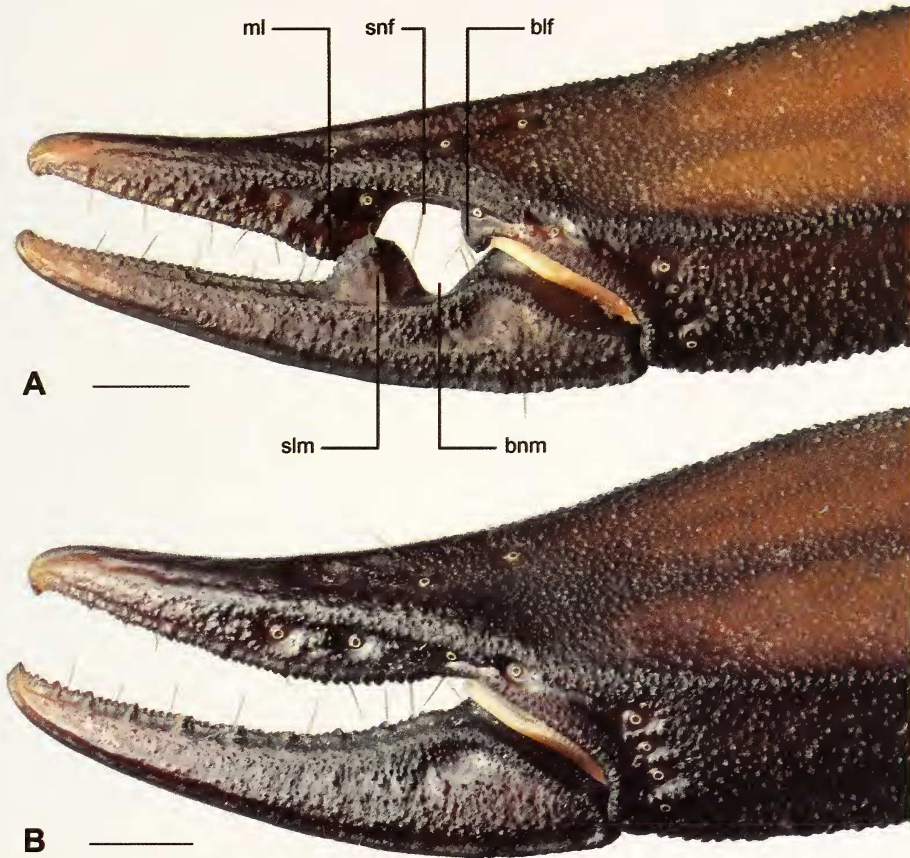


FIG. 6

Hormurus longimanus (Locket, 1995), pedipalp chela, retrolateral aspect, illustrating dentate margin of chela fingers. (A) Male (MNHG). (B) Female (MNHG). Abbreviations: blf (basal lobe, fixed finger), bnm (basal notch, movable finger), ml (median lobe), slm (suprabasal lobe, movable finger), snf (suprabasal notch, fixed finger). Scale, 1 mm.

carina distinct, granular. Chela manus (Fig. 5B-E): Dorsal secondary carina obsolete; digital carina distinct, granular, more strongly developed than external secondary carina; external secondary carina obsolete; ventroexternal carina granular to crenulate; ventromedian and ventrointernal carinae obsolete; internomedian carina distinct, granular. Pedipalp surface macrosculpture: Femur (Fig. 5L-O): Dorsal intercarinal surface finely and densely granular except distally; pro- and retrolateral intercarinal

FIG. 5

Hormurus longimanus (Locket, 1995), pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect, illustrating trichobothrial pattern. (A, F, K) Female (MNHG). (B-E, G-J, L-O) Male (MNHG). Scale, 2 mm.

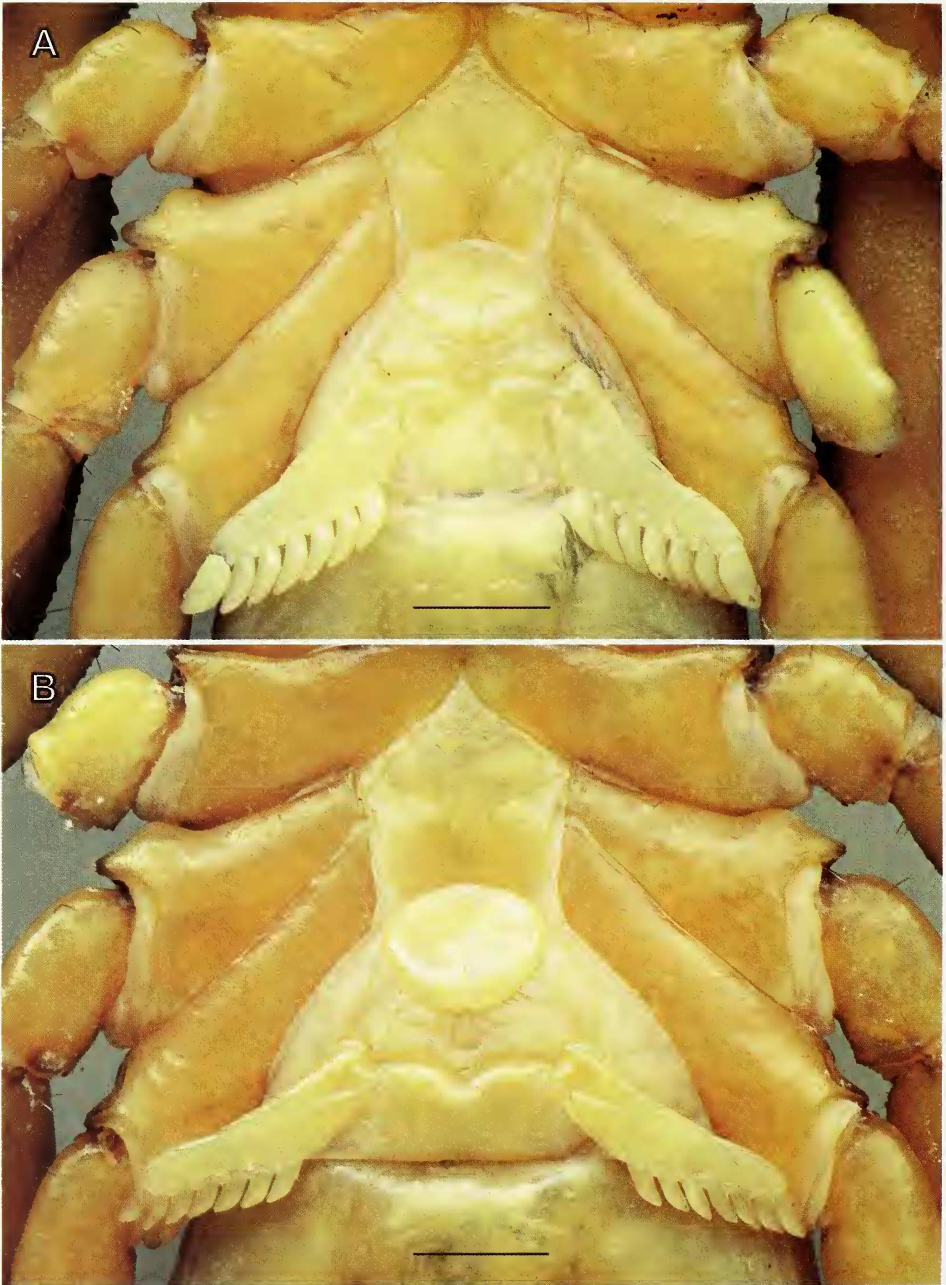


FIG. 7

Hormurus longimanus (Locket, 1995), coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Male (MNHG). (B) Female (MNHG). Scale, 1.5 mm.

surfaces at least sparsely granular; ventral intercarinal surface granular, distal extremity smooth. Patella (Fig. 5G-J): Dorsal, prolateral and retrolateral intercarinal surfaces finely and densely granular; ventral intercarinal surface sparsely granular, comprising a reticulated network of granules, distal margin smooth. Chela (Fig. 5B-E): Dorsal and retrolateral intercarinal surfaces of manus finely and densely granular; ventral intercarinal surface granular along pro- and retrolateral margins, smooth medially; prolateral intercarinal surface at least sparsely granular, slightly less so along ventral margin. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). **Trichobothria:** Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 5B-E, G-J, L-O). Patella: *d*₂ situated distal to patellar process; five *eb* trichobothria arranged in two groups, *eb*₁ and *eb*₂₋₅ or *eb*_{1/eb}₄₋₅ and *eb*₂₋₃; two *esb* trichobothria; two *em* trichobothria; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated at or slightly distal to midpoint; *Eb*₃ situated close to *Eb*₁₋₂; *Esb* situated midway between *Eb* series and *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with *V*₃ and *V*₄ separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 7A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 5/5 and 5/5 setiform macrosetae (Fig. 8D, E); ventromedian row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; unguis curved, shorter than telotarsus.

Genital operculum: Composed of two subtriangular sclerites (Fig. 7A).

Pectines: Slightly elongated, distal edge reaching but not surpassing distal edge of leg IV coxa (Fig. 7A); fulcra and two marginal lamellae present. Pectinal tooth count 6-8; teeth long and straight, entirely covered with sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth (Fig. 4A, E). Post-tergites: Posterior margins of I-VI sublinear, without distinct prominence (Fig. 4A, E); I-VI each with lateral transverse sulci; intercarinal surfaces of I and II finely and densely granular, more sparsely granular medially; intercarinal surfaces of III-VII finely and densely granular, uneven, with reticulated network of ridges and dimples. Respiratory stigmata (spiracles) of sternites IV-VI short, less than one third sternite width, and crescent-shaped, with distinct curve; sternite VII acarinate.

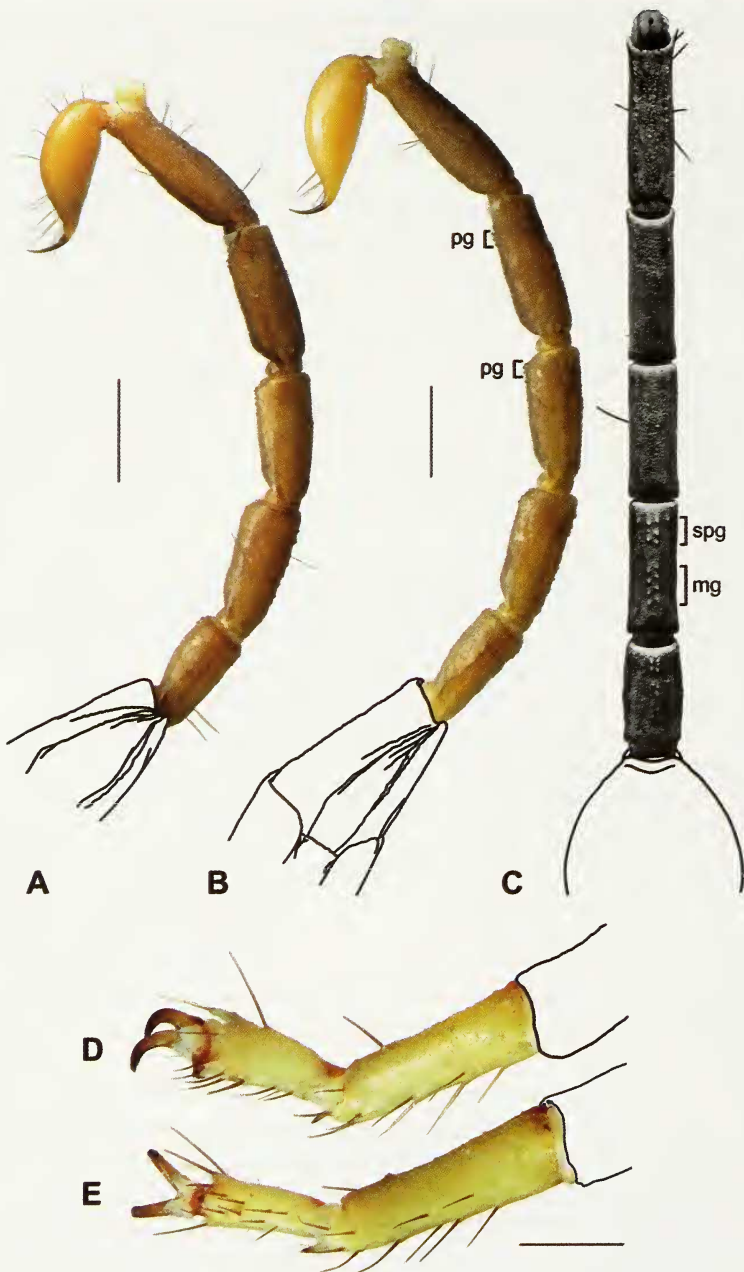


FIG. 8

Hormurus longimanus (Locket, 1995), metasoma and telson, lateral (A, B) and ventral (C) aspect, and left tarsus IV, retrolateral (D) and ventral (E) aspect. (A) Female (MNHG). (B-E) Male (MNHG). Abbreviations: mg (medial granules, ventro-submedian carinae), pg (posterior granules, dorso-submedian carinae), spg (subposterior granules, ventro-submedian carinae). Scale, 2 mm (A-C), 1 mm (D-E).

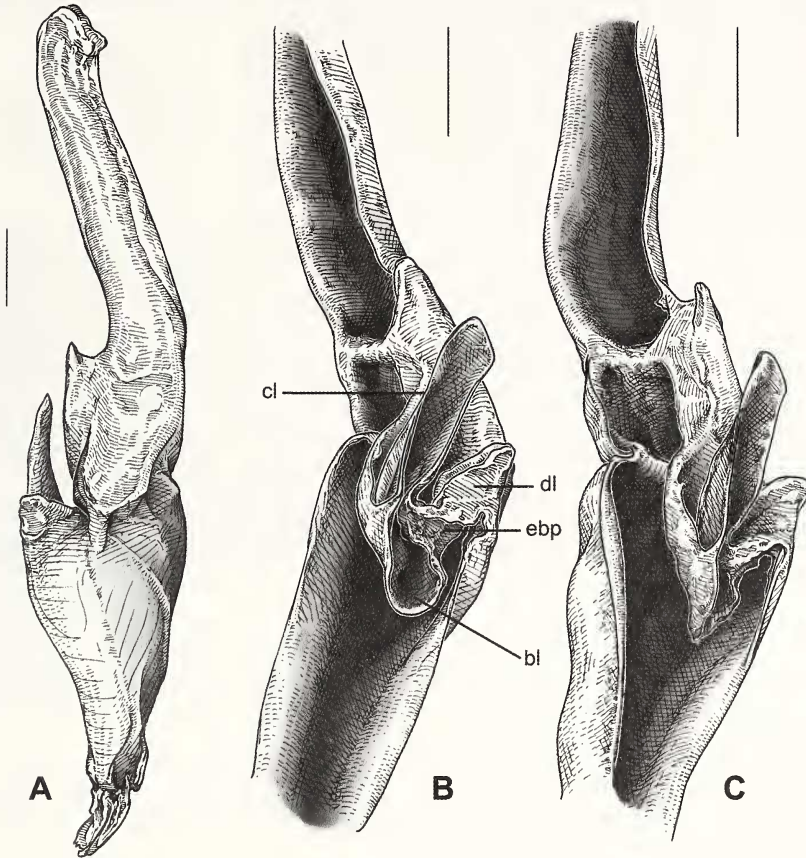


FIG. 9

Hormurus longimanus (Locket, 1995), male (AMNH), left hemispermatophore. (A) Dorsal aspect. (B, C) Detail of capsular region, ental (B) and ventral (C) aspect. Abbreviations: bl (basal lobe), cl (capsular lamella), dl (distal lobe), ebp (ental basal process). Scale, 0.5 mm.

Metasoma: Length similar to that of ♀ (Tab. 1), not flattened laterally (Fig. 8B, C), intercarinal surfaces finely and densely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae obsolete; dorsolateral, ventrolateral and ventro-submedian carinae distinct on at least some segments. Segment I: Width less than or equal to height (Tab. 1); dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carinae distinct; ventro-submedian carinae each with 4-6 spiniform granules medially, two or three sub-posteriorly, and none posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae each with one small spiniform granule subposteriorly and none

posteriorly; each ventro-submedian carina with four or five small spiniform granules medially, two or three small spiniform granules subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae distinctly larger than preceding granules; ventrolateral and ventro-submedian carinae weakly developed, sparsely granular, without spiniform granules. Segment V: Dorsal intercarinal surface sparsely granular; dorsolateral carinae obsolete; ventrolateral carinae weakly developed, indistinct in anterior half, granular in posterior half, granules becoming larger and spiniform posteriorly; ventromedian carina weakly developed, comprising a sparse row of spiniform granules; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 8B); vesicle surfaces smooth.

Hemispermaphore (Fig. 9): Distal lamina gently curved, slightly longer than basal part of hemispermaphore; distal crest absent; single laminar hook situated in basal third, at least more proximal than midpoint; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded only proximally and unfolded distally to flattened extremity (tip and base approximately same width); longitudinal carina on dorsal surface absent to weak; accessory hook and accessory lobe absent; lamellar tip situated proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory hook, carinae or crest. Basal lobe well developed, spoon-shaped, merging with ental basal process; ectal edge without accessory fold, forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: All segments noticeably shorter and more robust than in male (Figs 3B, D, 5A, F, K, 6B). Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Fig. 6B).

Carapace: Posteromedian surface less granular than in male (Fig. 4B, D).

Genital operculum: Oval to semi-oval, as wide as long, approximately same width as sternum (Fig. 7B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of coxa IV (Fig. 7B). Pectinal tooth count 5-7; teeth short and curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-VI smooth or nearly so (Fig. 4B, F); intercarinal surfaces of VII granular in posterior half only.

Metasoma: Intercarinal surfaces less granular than in male (Fig. 8A).

INTRASPECIFIC VARIATION: Pectinal tooth counts vary from six to eight in males, and from five to seven in females.

DISTRIBUTION: *Hormurus longimanus* inhabits the western escarpment of the Arnhem Land Plateau, Northern Territory, Australia (Fig. 10), and probably does not occur south of the South Alligator River. *Hormurus* has thus far not been recorded in nearby Nitmiluk National Park despite fieldwork conducted in the region by the senior author. It has also not been recorded in the northern Marrawal Plateau but it is likely to occur there.

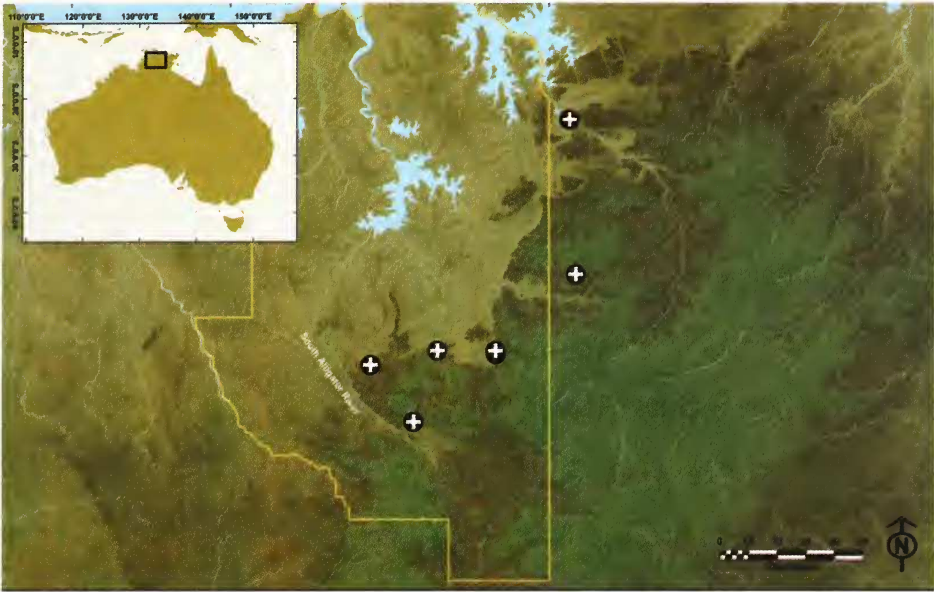


FIG. 10

Known localities of *Hormurus longimanus* (Locket, 1995) in the Northern Territory, Australia, with topography, major rivers including the South Alligator River, and boundary of the Kakadu National Park indicated.

ECOLOGY: An “archipelago” of *ca* 15,000 small patches of monsoon rainforest is scattered across the vast *Eucalyptus*-dominated landscape of predominantly savanna woodland in the Northern Territory of Australia (Russell-Smith *et al.*, 1992). Most of these patches are less than five hectares in extent, but occasionally they form extensive tracts along rivers and along the coast (Russell-Smith, 1991; Russell-Smith *et al.*, 1992). This fragmented habitat represents around 0.2% (300,000 hectares) of the total land area of the state (MPIGA, 2008). Two types of monsoon forest are recognised: wet monsoon forest occurs in areas with a perennial moisture supply, whereas dry monsoon forest occurs in well-drained areas, especially rocky areas, cliff lines and hilltops protected from recurring fires (Russell-Smith, 1991; Bowman *et al.*, 1991; Banfai & Bowman, 2006).

Hormurus longimanus is restricted to monsoon forests (mostly of the dry type) along the western edge of the Arnhem Land Plateau escarpment (Fig. 11B), which depend on orographic rainfall and the water-holding capacity of the bedrock in this predominantly rocky area (Fordyce *et al.*, 1997). The Middle-Proterozoic Kombolgie Sandstone Formation constitutes the major part of the Arnhem Plateau (Hoatson *et al.*, 2000; Johnson, 2004). The intergranular porosity of this quartz sandstone is very low (Emerson *et al.*, 1992) but the fracture system of the plateau is deep and extensive in the north and west, with an extended network of chasms, faults, gorges and fissures (Galloway, 1976; Snelling, 1992; Wyrwoll, 1992; see Fig. 11A). Rainwater accumulates in these weathered rock aquifers during the wet season, and gradually discharges



FIG. 11

Habitat of *Hormurus longimanus* (Locket, 1995) in the Northern Territory, Australia. (A) Patches of dry monsoon forest along the deeply dissected western escarpment of the Arnhem Plateau (photograph courtesy Ian Oswald-Jacobs, Parks Australia). (B) Dry monsoon forest on scree slope at Maguk.

to the surrounding habitats during the dry season. The aquifers maintain perennial seepage pools along the entire western escarpment throughout the dry season, creating a humid microclimate suitable to species like *H. longimanus* that cannot tolerate the drier conditions of the surrounding plains.

The habitat and habitus of this species are consistent with the lithophilous ecomorphotype (Prendini, 2001). All known specimens of this species were collected from narrow rock crevices and under stones near creeks and pools except the paratype, which was found under decaying bark. Specimens of lithophilous *Hormurus* species are occasionally found under the bark of logs or trees (L. Monod, personal observation). They are usually stray males that probably wandered away from the rocks seeking mates and found refuge in bark exfoliations that provide tight spaces like rock crevices.

CONSERVATION STATUS: Monsoon forest patches in the Top End of the Northern Territory are particularly vulnerable to disturbance associated with feral animals and fire (Russell-Smith & Bowman, 1992; Price *et al.*, 1995; Banfai & Bowman, 2006). In the Kakadu National Park, however, the forest patches are much larger than they were 40 years ago, mostly due to the removal of feral animals and efficient seasonal fire

management (Banfai & Bowman, 2006). The mining industry represents another potential threat to these unique habitats, especially in areas where forest patches depend on the natural discharge of ground water from nearby rock formations. Any alterations of the bedrock may have negative consequences for the water storage capacity of aquifers and ultimately for the surrounding humid habitats they sustain. As most of the known populations of *H. longimanus* lie within the boundaries of the Kakadu National Park, the species is currently not threatened by habitat destruction.

***Hormurus ischnoryctes* Monod & Prendini, n. spec.** Figs 12-21, 38B, D, Table 2

HOLOTYPE: QM; ♂; Australia, Queensland, Mount Mulligan cattle station, 16°50'S, 144°50'E; 16-17.VII.2006; 340 m, open woodland savanna, in vertical burrows 15-30 cm deep, with terminal chambers, G. Romand & L. Monod.

PARATYPES: AMNH, without registration number; 1 ♂, 4 ♀, 5 imm.; same data as holotype. – QM; 3 ♀, 4 imm.; same data as holotype. – AMCC LP 6639; 1 imm.; same data as holotype. – QM-S17140; 1 ♂; Mount Mulligan [16°51'Ex144°50'S]; 10.IX.1983; A. Williamson.

OTHER MATERIAL: MNHN RS 4209; 1 ♂, 1 ♀; Ravenshoe [145°29'0"S, 17°37'59"E]; VIII.1963; ca. 600 m, open *Eucalyptus* forest, marked cold season, low rainfall, H. St Girons.

ETYMOLOGY: The name *ischnoryctes* is constructed from the Greek words *ischnos* [thin, lean] and *oryktes* [digger]. It is an invariable noun in apposition and refers to the male pedipalps, which are unusually long and slender compared to those of other fossorial hormurids.

DIAGNOSIS: *Hormurus ischnoryctes* differs from other Australian species of the genus as follows. The base colouration of the cuticle is noticeably more reddish in *H. ischnoryctes* than in other species. The carapace is medially smooth or nearly so (only weakly granular around the median ocelli of the adult male) in *H. ischnoryctes*, whereas in other species it is granular, at least posteriorly. The prolateral process of the pedipalp patella is less developed in *H. ischnoryctes* than in other species except *H. ochyroscapter*. Mesosomal post-tergites I-IV of the adult male are smooth medially and granular laterally in *H. ischnoryctes* whereas in other species they are completely granular. The metasomal intercarinal surfaces of the female are smooth or nearly so in *H. ischnoryctes* whereas in other species they are at least sparsely granular.

DESCRIPTION OF ADULT MALE: *Colouration*: Dorsal surface of chelicera manus orange to brown; fingers dark brown to black (Fig. 12). Carapace reddish brown, with darker areas. Pedipalps red to reddish brown; carinae and fingers reddish brown to black. Legs orange to brown. Tergites brown to dark brown, slightly paler than carapace, without red tinge. Coxapophyses, sternum, genital operculum, pectines and sternites pale orange to brown. Metasoma brown to dark brown. Telson orange to pale brown; aculeus reddish-black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma, and metasoma finely punctate.

Carapace: Anterior margin with shallow median notch (Fig. 14A). Anterior furcated suture and sulci distinct. Median ocular tubercle situated anteromedially, at least slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated by at least half the diameter of a median ocellus. Three pairs of lateral ocelli,



FIG. 12

Hormurus ischnoryctes n. spec., male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

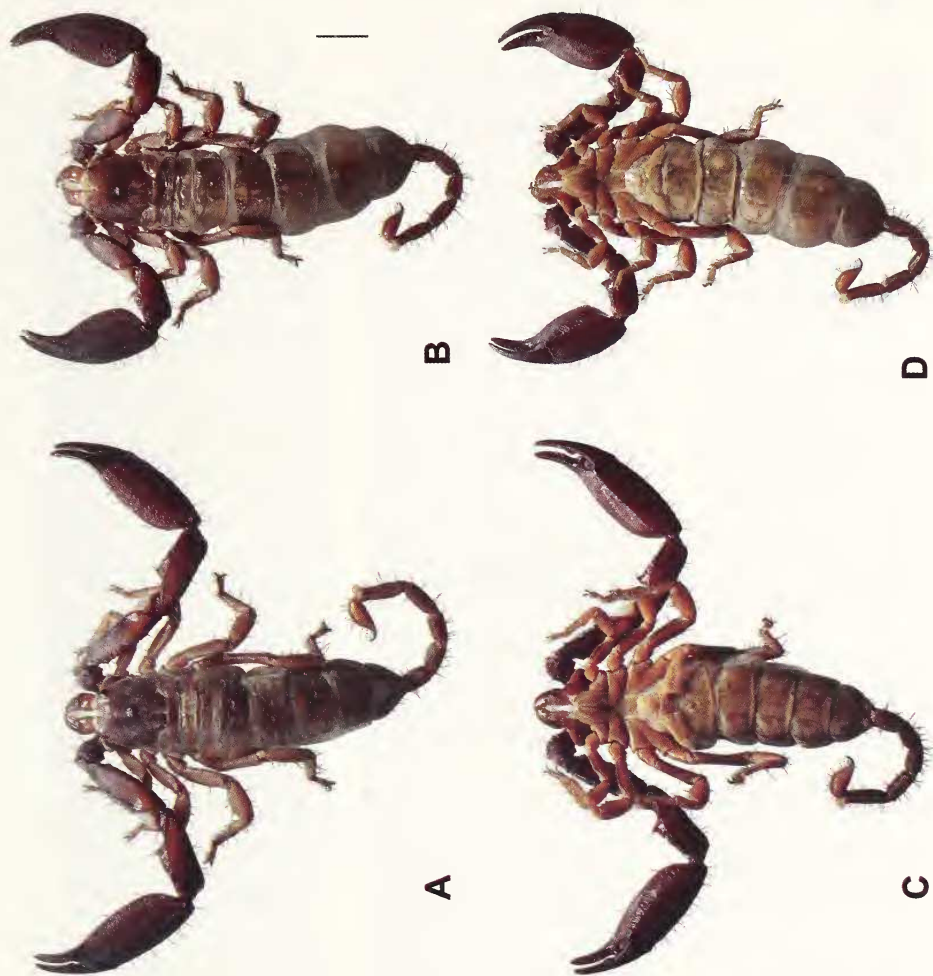


FIG. 13

Hormurus ischnoryctes n. spec., habitus, dorsal (A, B) and ventral (C, D) aspect. (A, C) Holotype male (QM). (B, D) Paratype female (QM). Scale, 5 mm.

equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces of frontal lobes smooth; surfaces adjacent to anterior furcated and median longitudinal sulci finely granular (Fig. 14C); median and lateral surfaces finely and at least sparsely granular; posteromedian surfaces smooth.

Chelicerae: Median and basal teeth of fixed finger fused into a bicuspid. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: All segments slightly elongated (Figs 12, 13A, C, 15B-E, G-J, L-O, 16A), with femur length slightly longer than carapace length (Tab. 2). Chela almost

TABLE 2. *Hormurus ischnoryctes* n. sp., measurements (in mm) of adult males and females.

Sex	Holotype		Paratype		Paratype	
	♂	♂	♂	♀	♀	♀
Repository	QM	QM-S 17140	AMNH	QM	QM	AMNH
Locality	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station
Total length	55.0	48.0	46.0	59.0	58.0	51.0
Carapace, length	7.2	7.6	6.8	8.1	7.9	7.8
Carapace, anterior width	5.3	5.5	4.8	5.9	5.5	5.6
Carapace, posterior width	7.6	8.7	7.2	8.4	7.8	7.7
Chela, length	17.2	17.9	15.1	16.5	14.9	14.6
Chela manus, width	4.7	4.9	4.5	5.7	5.5	5.3
Chela manus, height	3.1	3.1	2.8	3.7	3.4	3.1
Chela movable finger, length	7.6	8.5	6.9	8.4	7.6	7.1
Patella, length	9.1	9.2	7.8	7.9	7.3	7.0
Patella, width	3.6	3.6	3.1	3.8	3.7	3.4
Femur, length	9.0	9.5	7.8	7.4	7.1	6.8
Femur, width	3.0	3.0	2.7	3.2	3.0	3.1
Metasomal segment I, length	3.5	2.9	3.2	3.5	3.0	3.1
Metasomal segment I, width	1.9	2.1	1.6	2.0	1.9	2.0
Metasomal segment V, length	4.4	4.2	4.3	4.6	4.2	4.2
Metasomal segment V, width	1.2	1.4	1.1	1.3	1.3	1.3
Metasomal segment V, height	1.48	1.46	1.25	1.51	1.38	1.45
Telson vesicle, width	1.64	1.6	1.41	1.58	1.41	1.44
Telson vesicle, height	1.7	1.45	1.6	1.69	1.6	1.57

asetose. **Chela fingers:** Dentate margins of fixed and movable fingers linear (without lobe and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe well developed, conical; suprabasal notch distinct and deep (Fig. 16A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, wider than high, gently rounded dorsally and lacking a sharp conical tooth, not overlapping fixed finger; suprabasal lobe and corresponding suprabasal notch of fixed finger contiguous, no proximal gap or at most a reduced gap evident when fingers closed. **Pedipalp carinae:** Femur (Fig. 15L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal carina vestigial, without spiniform granules or with one large spiniform granule situated medially on segment; internomedian ventral carina vestigial, comprising two large spiniform granules situated proximally and medially on segment; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 15G-J): Prolateral process distinct but reduced, forming single large spine; internodorsal and dorsomedian carinae distinct; dorsoexternal carina obsolete; externomedian carina granular; ventroexternal carina distinct, costate-granular. Chela manus (Fig. 15B-E): Dorsal secondary carina obsolete; digital carina distinct, granular, more strongly developed than external secondary carina; external secondary carina obsolete;

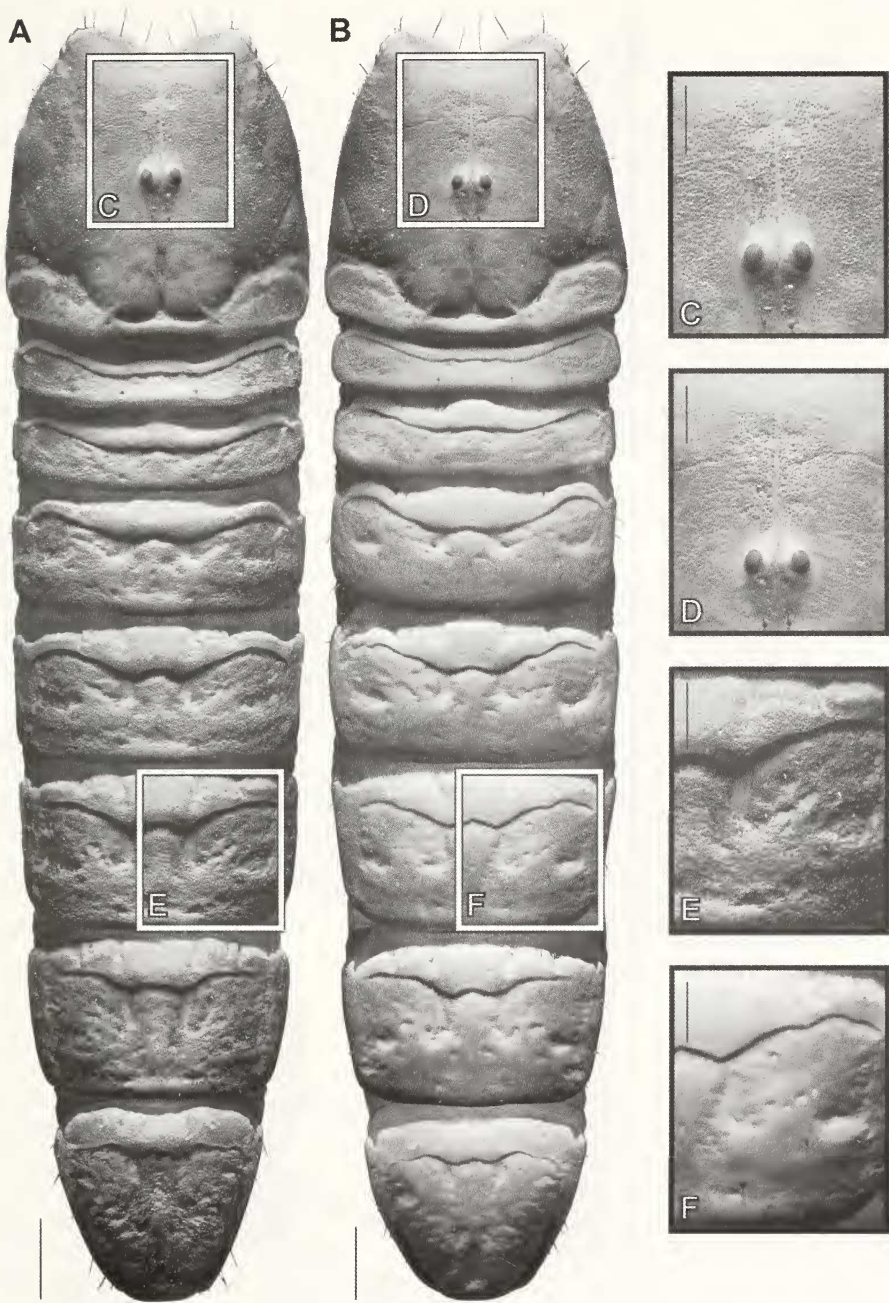


FIG. 14

Hormurus ischnoryctes n. spec., carapace and mesosomal tergites illustrating ornamentation and macrostructure of cuticle (A, B), with detailed view of carapace (C, D) and tergite V (E, F), dorsal aspect. (A, C, E) Holotype male (QM). (B, D, F) Paratype female (QM). Scale, 2 mm (A, B), 1 mm (C-F).

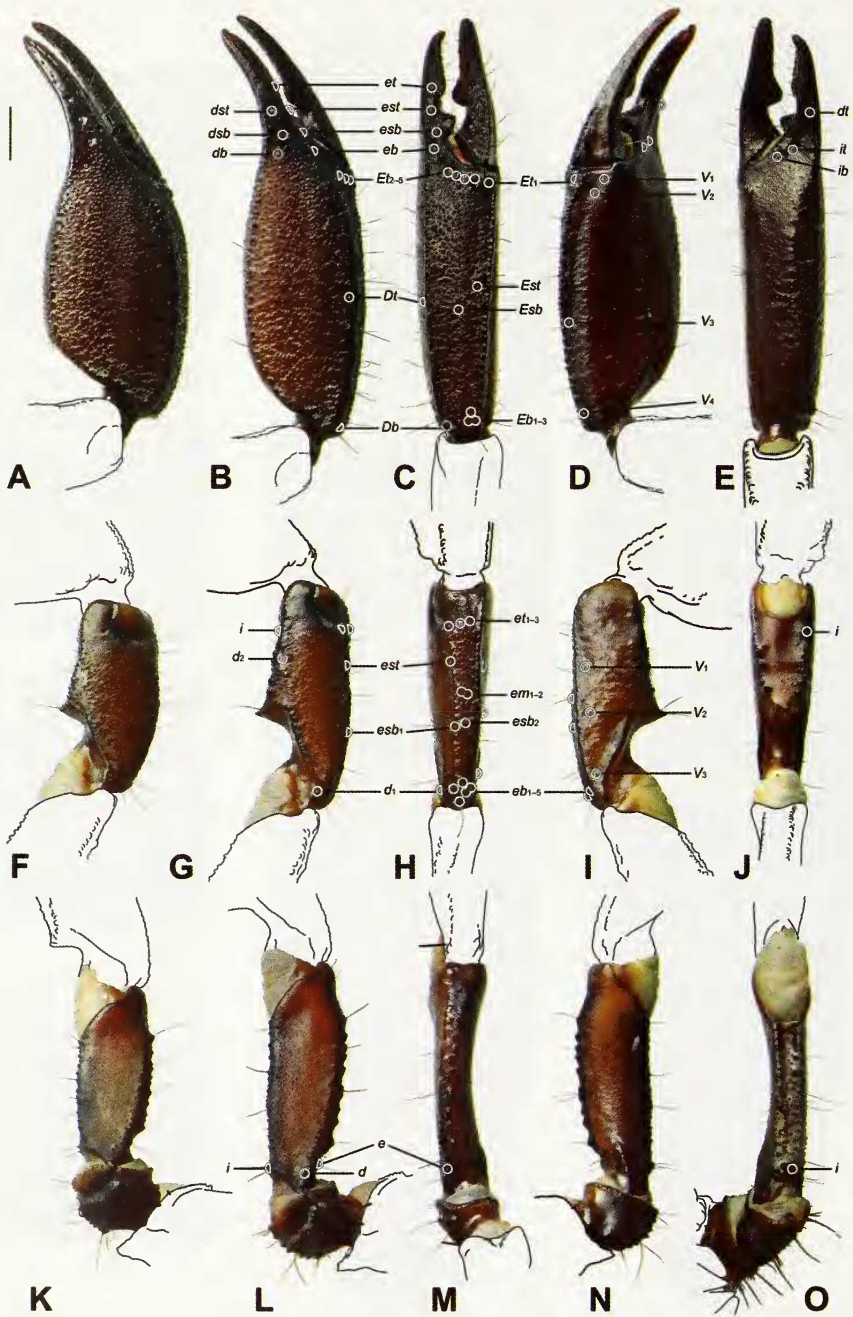


FIG. 15

Hormurus ischnoryctes n. spec., pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect illustrating trichobothrial pattern. (A, F, K) Paratype female (QM). (B-E, G-J, L-O) Holotype male (QM). Scale, 2 mm.

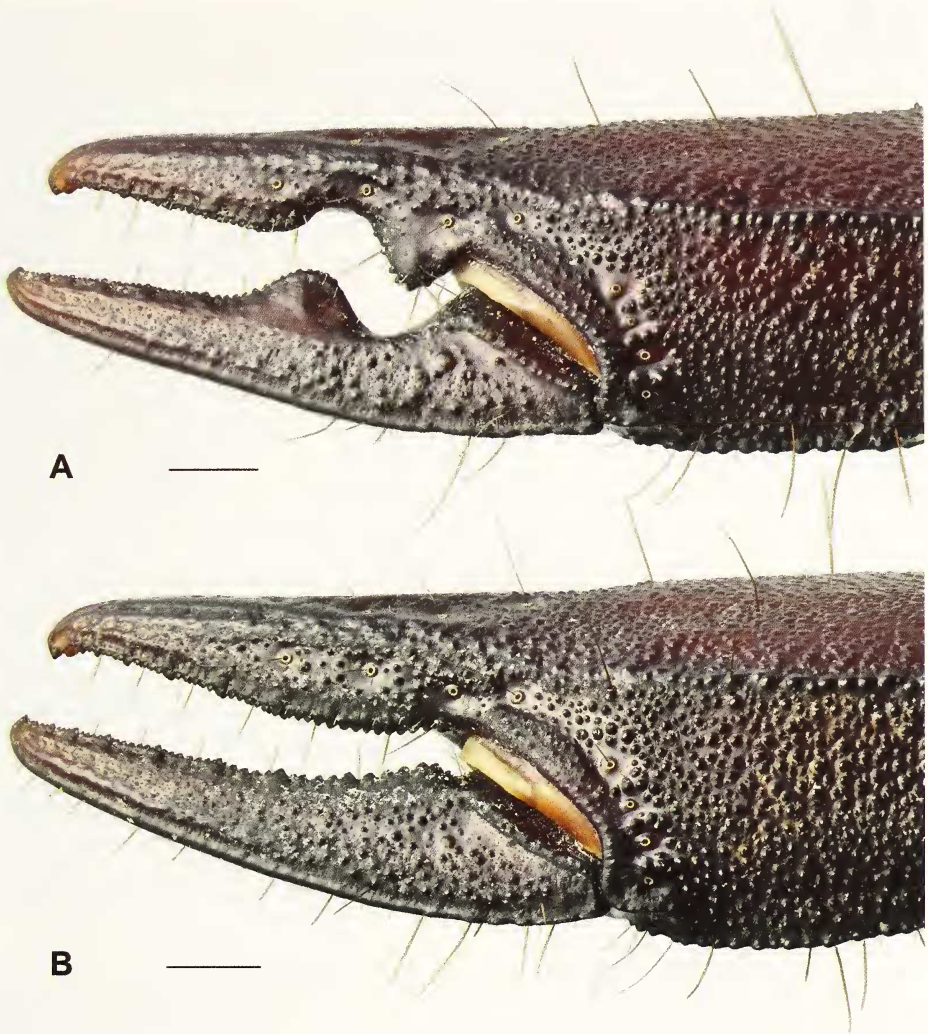


FIG. 16

Hormurus ischnoryctes n. spec., pedipalp chela, retrolateral aspect illustrating dentate margin of chela fingers. (A) Holotype male (QM). (B) Paratype female (QM). Scale, 1 mm.

ventroexternal carina granular to crenulate; ventromedian carina obsolete; ventro-internal carina reduced to row of small granules; internomedian carina distinct, sparsely granular. Pedipalp surface macrosculpture: Femur (Fig. 15L-O): Dorsal intercarinal surface densely granular except distally; pro- and retrolateral intercarinal surfaces at least sparsely granular; retrolateral intercarinal surface smooth or nearly so ventrally; ventral intercarinal surface granular proximally, smooth distally. Patella (Fig. 15G-J): Dorsal and retrolateral intercarinal surfaces granular or at least comprising a reticulated network of granules; ventral intercarinal surface sparsely granular,

distal extremity smooth; prolateral intercarinal surface sparsely granular proximally, usually less so in distal half. Chela (Fig. 15B-E): Dorsal intercarinal surface of manus densely granular, comprising medium-sized granules; retrolateral intercarinal surface granular; ventral intercarinal surface granular along pro- and retrolateral margins only, smooth medially; prolateral intercarinal surface granular. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). Trichobothria: Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 15B-E, G-J, L-O). Patella d_2 situated distal to patellar process; five *eb* trichobothria arranged in two groups, eb_1 and eb_{2-5} or eb_1/eb_{4-5} and eb_{2-3} ; two *esb* trichobothria; two *em* trichobothria; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated in proximal third; Eb_3 situated close to Eb_{1-2} ; *Esb* situated distal to *Eb* series and close to *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with V_3 and V_4 separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 17A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 5/4-5, 5-6/5 setiform macrosetae, respectively (Fig. 18D, E); ventro-median row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; unguis curved, shorter than telotarsus.

Genital operculum: Composed of two subtriangular sclerites (Fig. 17A).

Pectines: Slightly elongated, distal edge reaching but not surpassing distal edge of leg IV coxa (Fig. 17A); fulcra and three marginal lamellae present. Pectinal tooth count 8-10; teeth long and straight, entirely covered by sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth (Fig. 14A, E). Posterior margins of post-tergites I-VII sublinear, without distinct prominence (Fig. 14A, E); I-VI each with lateral transverse sulci; intercarinal surfaces of I-IV smooth medially, finely granular posterolaterally, at least sparsely so; intercarinal surfaces of III-VII uneven, with a distinct reticulated network of ridges and dimples; intercarinal surfaces of V-VII finely granular, at least sparsely so. Respiratory stigmata (spiracles) of sternites IV-VI short, less than one third sternite width and crescent-shaped, with distinct curve; sternite VII acarinate.

Metasoma: Length similar to that of ♀ (Tab. 2), not flattened laterally (Fig. 18B, C), intercarinal surfaces sparsely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae obsolete; dorsolateral, ventrolateral and ventro-submedian carinae



FIG. 17

Hormurus ischnoryctes n. spec., coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Holotype male (QM). (B) Paratype female (QM). Scale, 1.5 mm.

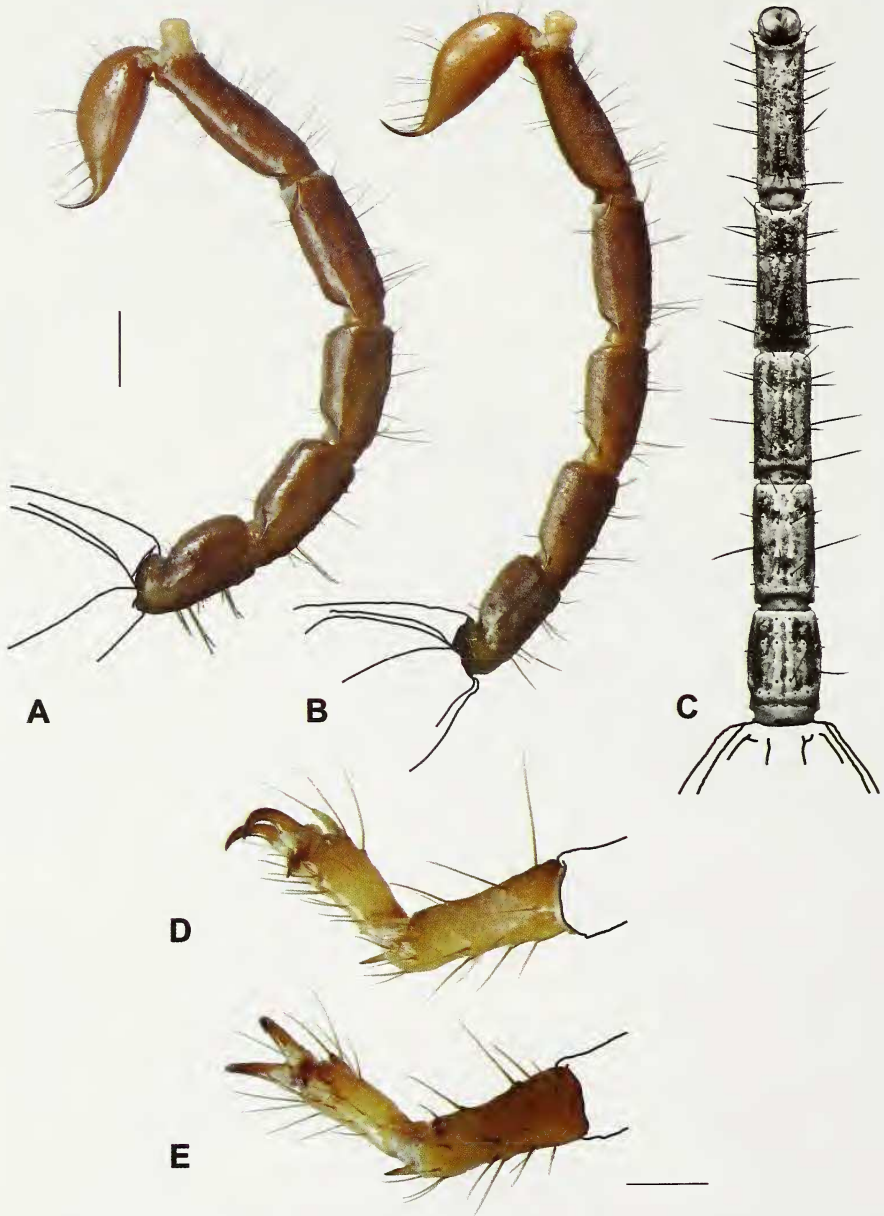


FIG. 18

Hormurus ischnoryctes n. spec., metasoma and telson, lateral (A, B) and ventral (C) aspect, and left tarsus IV, retrolateral (D) and ventral (E) aspect. (A) Paratype female (QM). (B-E) Holotype male (QM). Scale, 2 mm (A-C), 1 mm (D-E).

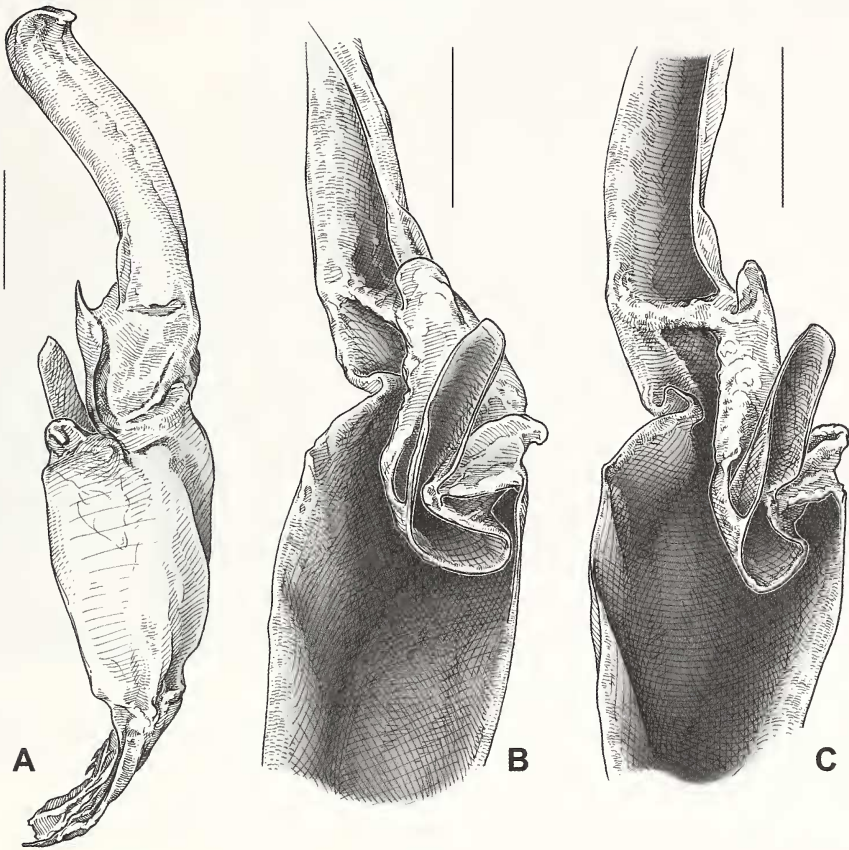


FIG. 19

Hormurus ischnoryctes n. spec., paratype male (AMNH), left hemispermatophore. (A) Dorsal aspect. (B, C) Detail of capsular region, ental (B) and ventral (C) aspect. Scale, 1 mm.

distinct on at least some segments. Segment I: Width less than or equal to height (Tab. 2); dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carinae distinct; ventro-submedian carinae each with one or two weakly developed spiniform granules medially, one or two subposteriorly, and none posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae without spiniform granules; ventro-submedian carinae each with one or two spiniform granules medially, 1-3 subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral and ventro-submedian carinae weakly developed, sparsely granular, without spiniform granules. Segment V: Dorsal intercarinal surface sparsely granular;



FIG. 20

Known localities of *Hormurus ischnoryctes* n. spec. in northern Queensland, Australia, with topography indicated.

dorsolateral carinae obsolete; ventrolateral carinae indistinct in anterior half, weakly developed, comprising few larger spiniform granules in posterior half; ventromedian carina weakly developed, comprising a sparse row of spiniform granules in anterior half, indistinct posteriorly; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 18B); vesicle surfaces smooth.

Hemispermatothore (Fig. 19): Distal lamina curved, slightly longer than basal part; distal crest absent; well developed single laminar hook situated in basal third; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded proximally and unfolded distally to a flattened extremity (tip and base approximately the same width); longitudinal carina on dorsal surface absent to weak; accessory hook and accessory lobe absent; lamellar tip situated slightly proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory carinae or crest, and with moderately developed, proximad-oriented accessory hook on ental surface. Basal lobe well developed, spoon-shaped, merging with ental basal process; ectal edge without accessory fold, forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: All segments slightly shorter and more robust than in male (Figs 13B, D, 15A, F, K, 16B). Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Fig. 16B).



FIG. 21

Habitat of *Hormurus ischnoryctes* n. spec. in northern Queensland, Australia. Open savanna woodland at the base of the Ngarrabullgan mesa.

Carapace: Median surface smooth or nearly so (Fig. 14B, D).

Genital operculum: Oval to semi-oval, as wide as long, approximately same width as sternum (Fig. 17B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of leg IV coxa (Fig. 17B). Pectinal tooth count 7-9; teeth short and curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-VII smooth or nearly so (Fig. 14B, F); intercarinal surfaces of III-VII almost even, reticulate network of ridges and dimples obsolete.

Metasoma: Intercarinal surfaces smooth or nearly so (Fig. 18A).

INTRASPECIFIC VARIATION: Pectinal tooth counts vary from eight to ten in males, and from seven to nine in females.

DISTRIBUTION: *Hormurus ischnoryctes* was collected from open savanna woodlands west of Mareeba and the Atherton Tablelands in the North Queensland Highlands Province of Queensland, Australia (Fig. 20).

ECOLOGY: *Hormurus ischnoryctes* was collected at the base of a large Mesozoic sandstone mesa that dominates the surrounding Queensland savanna. The Pepper Pot Sandstone, dating to the early Triassic, forms the monolithic unit of this escarpment

(Bultitude *et al.*, 1997; Withnall *et al.*, 1997). As with the Arnhem Plateau, this geological formation provides orographic moisture to the surrounding habitats throughout the dry months (May to October), creating a more humid microclimate along its base and slopes that supports scattered patches of mesic vine thicket. These humid habitats form a stark contrast to the surrounding semi-arid open sclerophyll woodlands (Fig. 21) and are similar in that respect to the monsoon forest patches of the Kakadu National Park, inhabited by *H. longimanus*. *Hormurus ischnoryctes* was not collected in the vine thicket patches but at the base of the mesa, in the vicinity of a perennial pool. The burrows of this fossorial species are vertical and about 15-30 cm deep, with a slit-like entrance and an enlarged terminal chamber (Fig. 38B, D). The habitat and habitus are consistent with the pelophilous ecomorphotype (Prendini, 2001).

CONSERVATION STATUS: The only known population of this species is located on privately owned land where cattle farming is the dominant land-use, but in an area where grazing does not occur. However, the population appears to be at risk from other human activities. The coal basement of the geological formation that sustains the population was mined from 1910 to 1957, until this energy supply was replaced by a hydro-electric scheme. However, a major energy company recently resuscitated the exploitation of this coal deposit, and large-scale mining is expected to resume in the near future. No other populations of this species are known to occur within protected areas. Because of the restricted distribution of the only known population and the imminent threat of habitat destruction, it is recommended that *H. ischnoryctes* be placed on the IUCN Red List of vulnerable species (IUCN, 2001).

***Hormurus macrochela* Monod, n. spec.**

Figs 22-31, Table 3

Liocheles waigiensis: L. E. Koch, 1977 (misidentification, part): 171, 172. – Volschenk *et al.*, 2001: 162 (misidentification, part).

HOLOTYPE: QM-S59212; ♂; Australia, Queensland, Palm Island, site 4, 18°40'S, 146°40'E; 22.II.2001; 100 m, rainforest, G. B. Monteith.

PARATYPES: QM-S17042; 1 ♀, 3 imm.; Palm Island, 18°50'S, 146°40'E; L. Bancroft. – QM S17088; 1 imm.; idem; IX.1923; H. A. Longman. – QM-S59206; 1 ♂, 1 ♀; Palm Island, site 1, 18°50'S, 146°40'E; 20-21.II.2001; 450 m, rainforest, G. B. Monteith.

OTHER MATERIAL: NHML 1890.7.1.216-221; 1 ♂; Australia; Keyserling. – NHML 1925.IX.12.1-4; 1 ♂ 1 ♀, 2 imm.; Magnetic Island [19°08'19"S, 146°50'04"E]; G. F. Hill. – ESV 3370; 1 ♂; VI.1992; vine forest, E. S. Volschenk. – MHNG, without registration number; Magnetic Island, 19°10'S, 146°50'E; 4 ♂, 7 ♀, 2 imm.; 28-29.XI.2004; 41 m, vine thicket along dry creek, in rock crevices (very narrow or in between stones), R. Wyss & L. Monod. – QM; 1 ♂, 1 ♀; same data as previous record. – AMCC LP 5555; 1 imm.; same data as previous record. – NTM, without registration number; 1 ♀; Orpheus Island [18°37'20"S, 146°29'57"E]; XI.1982; R. Tuesley.

ETYMOLOGY: The name *macrochela* is constructed from the Greek words *makros* [long] and *chela* [claw]. It is an invariable noun in apposition and refers to the extreme elongation of the male pedipalps.

DIAGNOSIS: *Hormurus macrochela* differs from other Australian hormurids as follows. Sexual dimorphism of the pedipalps is more pronounced in *H. macrochela* than in other species except *H. longimanus*. The ventrointernal carina of the pedipalpal chela manus is distinct and coarsely granular in *H. macrochela* whereas it is weakly developed and smooth or nearly so in other species except *Liocheles litodactylus*



FIG. 22

Hormurus macrochela n. spec., male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.



FIG. 23

Hormurus macrochela n. spec., habitus, dorsal (A, B) and ventral (C, D) aspect. (A, C) Holotype male (QM-S59212). (B, D) Paratype female (QM-S59206). Scale, 10 mm.

Monod & Volschenk, 2004. The pedipalp chela trichobothrium *Esb* is situated close to trichobothrium *Est* in *H. macrochela* whereas it is situated midway between the *Eb* group of trichobothria and *Est* in other species except *H. ischnoryctes*. The mesosomal post-tergite VII is granular at least posteriorly in *H. macrochela* but smooth or nearly so in other species except *H. longimanus*. An accessory hook, present on the ental surface of the distal lobe of the hemispermatophore capsule in *H. macrochela*, is absent in other species except *H. ischnoryctes* and *H. ochyroscapter*.

DESCRIPTION OF ADULT MALE: *Colouration*: Dorsal surface of chelicera manus orange, with darker infuscation; fingers dark brown to black (Fig. 22). Carapace dark

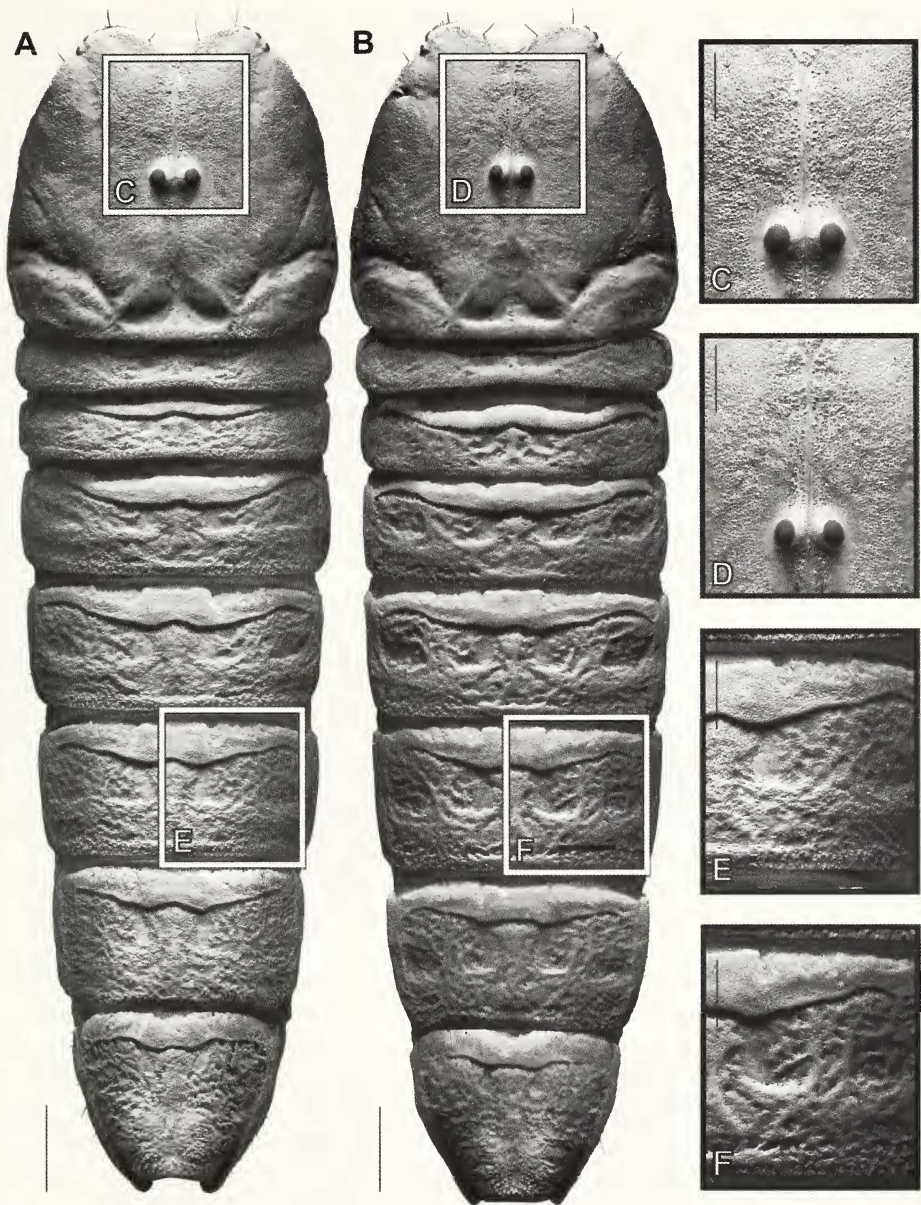


FIG. 24

Hormurus macrochela n. spec., carapace and mesosomal tergites, illustrating ornamentation and macrosculpture of cuticle (A, B), with detailed view of carapace (C, D) and tergite V (E, F), dorsal aspect. (A, C, E) Paratype male (QM-S59206). (B, D, F) Paratype female (QM-S59206). Scale, 3 mm (A, B), 1.5 mm (C-F).

reddish brown to black. Pedipalps dark reddish brown to black; carinae and fingers black. Legs pale brown. Tergites brown, paler than carapace. Coxapophyses, sternum, genital operculum, pectines and sternites orange to pale brown. Metasoma dark reddish brown to black. Telson orange; aculeus reddish-black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma, and metasoma finely punctate.

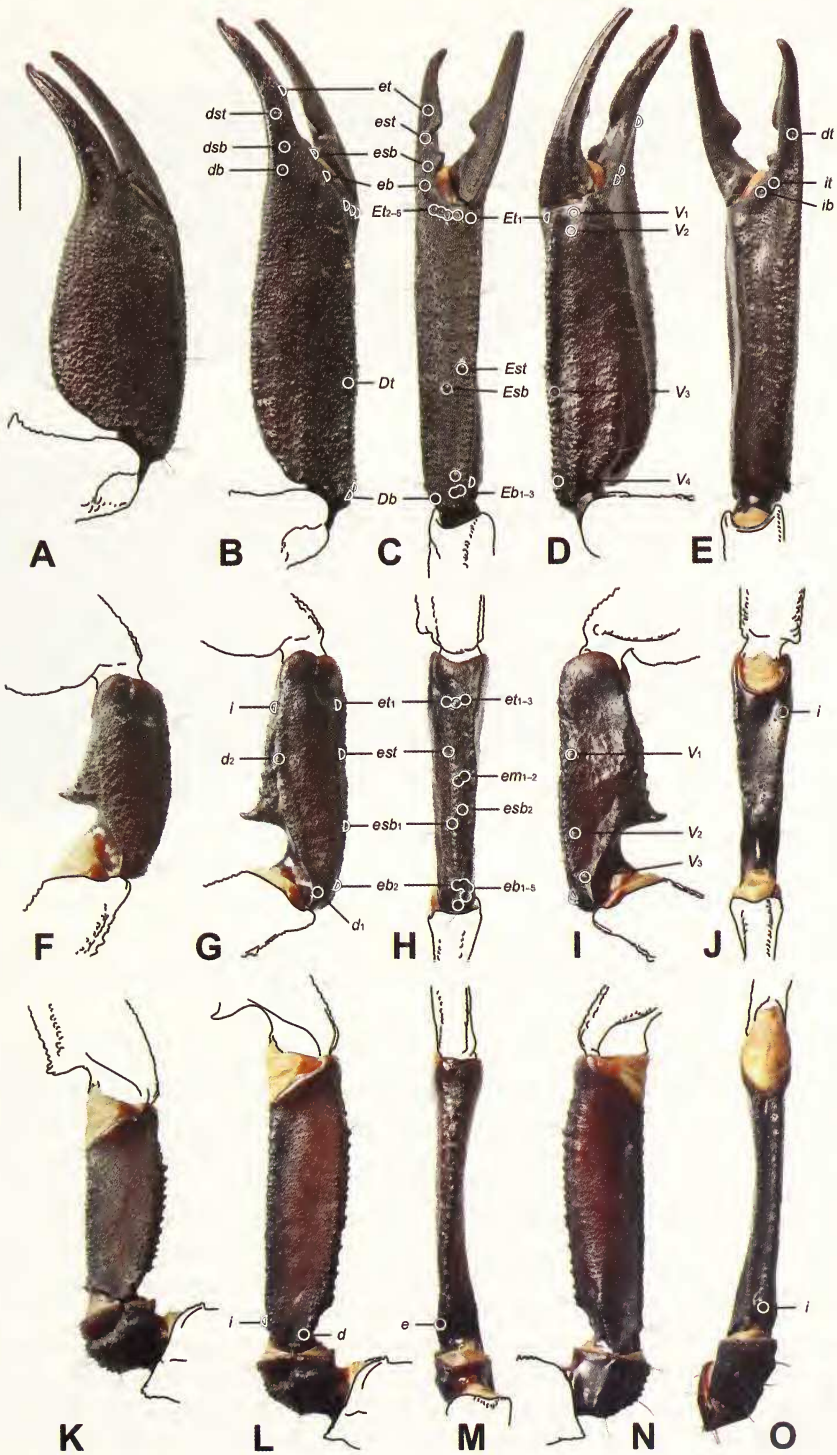
Carapace: Anterior margin with shallow median notch (Fig. 24A). Anterior furcated sutures and sulci distinct. Median ocular tubercle situated anteromedially, slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated by at least half the diameter of a median ocellus. Three pairs of lateral ocelli, equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces finely granular, at least sparsely so, except anteromedially, with frontal lobes smooth and fine granulation restricted to surfaces adjacent to anterior furcated and median longitudinal sulci (Fig. 24C).

Chelicerae: Median and basal teeth of fixed finger fused into a bicuspid. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: Segments very long and slender (Figs 22, 23A, C, 25B-E, G-J, L-O, 26A), with femur length approximately 1.5 times carapace length (Tab. 3). Chela almost asetose. Chela fingers: Dentate margins of fixed and movable fingers linear (without lobe and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe well developed, conical; suprabasal notch distinct and deep (Fig. 26A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, wider than high, gently rounded dorsally and lacking a sharp conical tooth, not overlapping fixed finger; suprabasal lobe and corresponding suprabasal notch on fixed finger contiguous, no proximal gap or at most a reduced gap evident when fingers closed. Pedipalp carinae: Femur (Fig. 25L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal and internomedian ventral carinae obsolete, without spiniform granules; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 25G-J): Prolateral process strongly developed, forming a prominent median spine; internodorsal and dorsomedian carinae distinct; dorsoexternal carina obsolete; externomedian carina granular; ventroexternal carina distinct, granular. Chela manus (Fig. 25B-E): Dorsal secondary carina obsolete; digital carina distinct, granular, more strongly developed than external secondary carina; external secondary carina obsolete; ventroexternal carina granular to crenulate; ventromedian carina obsolete;

FIG. 25

Hormurus macrochela n. spec., pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect, illustrating trichobothrial pattern. (A, F, K) Paratype female (QM-S59206). (B-E, G-J, L-O) Holotype male (QM-S59212). Scale, 3 mm.



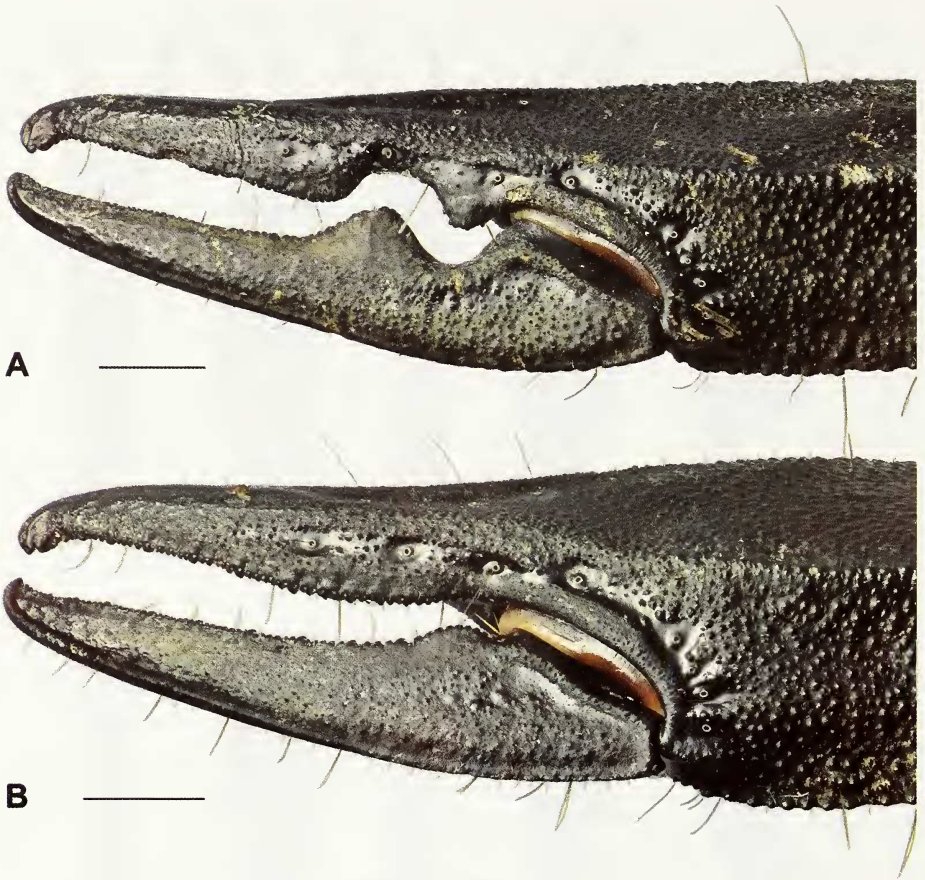


FIG. 26

Hormurus macrochela n. spec., pedipalp chela, retrolateral aspect, illustrating dentate margin of chela fingers. (A) Holotype male (QM-S59212). (B) Paratype female (QM-S59206). Scale, 2 mm.

ventrointernal carina distinct, costate-granular; internomedian carina distinct, granular, more strongly developed than ventrointernal carina. Pedipalp surface macrosculpture: Femur (Fig. 25L-O): Dorsal intercarinal surface densely granular except distally; pro- and retrolateral intercarinal surfaces at least sparsely granular; ventral intercarinal surface granular, distal extremity smooth. Patella (Fig. 25G-J): Dorsal, retrolateral and ventral intercarinal surfaces granular or at least comprising a reticulated network of granules; prolateral intercarinal surface at least sparsely granular in proximal half, usually less so in distal half. Chela (Fig. 25B-E): Dorsal and retrolateral intercarinal surfaces of manus densely granular; prolateral and ventral intercarinal surfaces at least sparsely granular. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). Trichobothria: Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 25B-E, G-J, L-O).

TABLE 3. *Hormurus macrochela* n. sp., measurements (in mm) of adult males and females.

Sex	Holotype	Paratype		Paratype	Paratype	
	♂	♂	♂	♀	♀	♀
Repository	QM-S5921	QM-S59206	MHNG	QM-S59206	QM-S17042	MHNG
Locality	Palm Island	Palm Island	Magnetic Island	Palm Island	Palm Island	Magnetic Island
Total length	66.0	61.0	48.0	70.0	64.0	55.0
Carapace, length	10.3	10.0	7.8	10.5	10.9	9.0
Carapace, anterior width	6.5	6.5	4.9	6.4	7.1	5.6
Carapace, posterior width	11.1	10.5	8.2	11.3	12.5	9.6
Chela, length	30.0	27.5	18.9	23.6	26.2	20.0
Chela manus, width	6.2	5.7	4.3	7.5	8.1	6.5
Chela manus, height	3.4	3.5	2.6	4.4	4.6	3.4
Chela movable finger, length	13.4	11.8	8.7	11.9	12.8	9.9
Patella, length	15.9	14.0	10.3	11.2	12.3	9.8
Patella, width	5.0	5.0	3.7	5.1	5.5	4.4
Femur, length	17.9	16.3	11.5	11.6	13.3	10.5
Femur, width	4.8	4.5	3.4	4.5	4.8	3.9
Metasomal segment I, length	3.9	3.6	2.5	3.4	4.2	3.0
Metasomal segment I, width	2.6	2.6	1.7	2.5	2.7	2.2
Metasomal segment V, length	6.4	5.8	4.8	5.7	5.7	4.6
Metasomal segment V, width	1.5	1.6	1.4	1.6	1.8	1.5
Metasomal segment V, height	1.8	1.9	1.5	1.8	2	1.6
Telson vesicle, width	1.6	1.6	1.4	1.7	1.7	1.5
Telson vesicle, height	2.0	2.1	1.5	1.8	2.1	1.8

Patella: d_2 situated distal to patellar process; five *eb* trichobothria arranged in two groups, eb_1 and eb_{2-5} or eb_1/eb_{4-5} and eb_{2-3} ; two *esb* trichobothria; two *em* trichobothria; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated in proximal third; Eb_3 situated close to Eb_{1-2} ; *Esb* situated distal to *Eb* series and close to *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with V_3 and V_4 separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 27A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 5/5, and 5/5 setiform macrosetae, respectively (Fig. 28D, E); ventromedian row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; ungues curved, shorter than telotarsus.

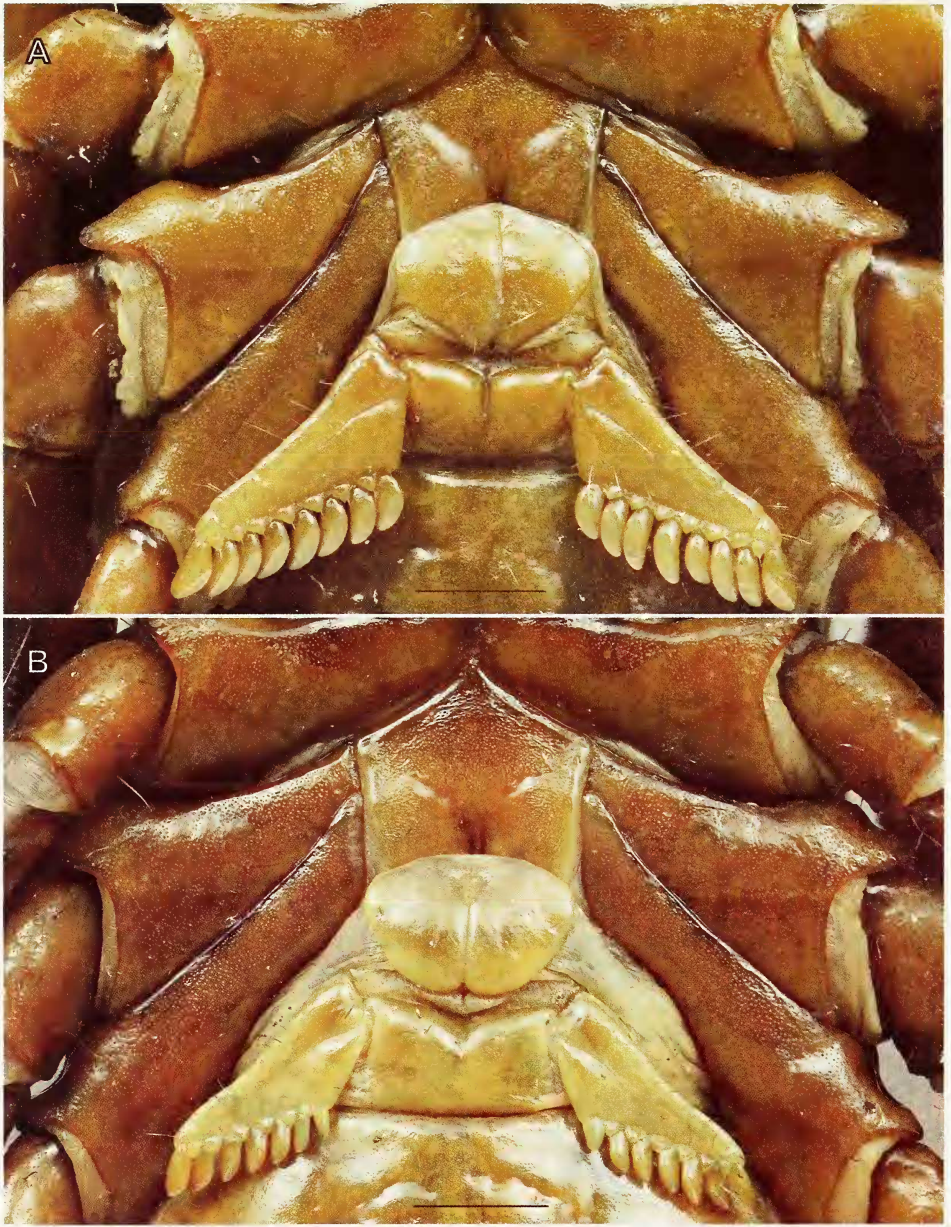


FIG. 27

Hormurus macrochela n. spec., coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Holotype male (QM-S59212). (B) Paratype female (QM-S59206). Scale, 2 mm.

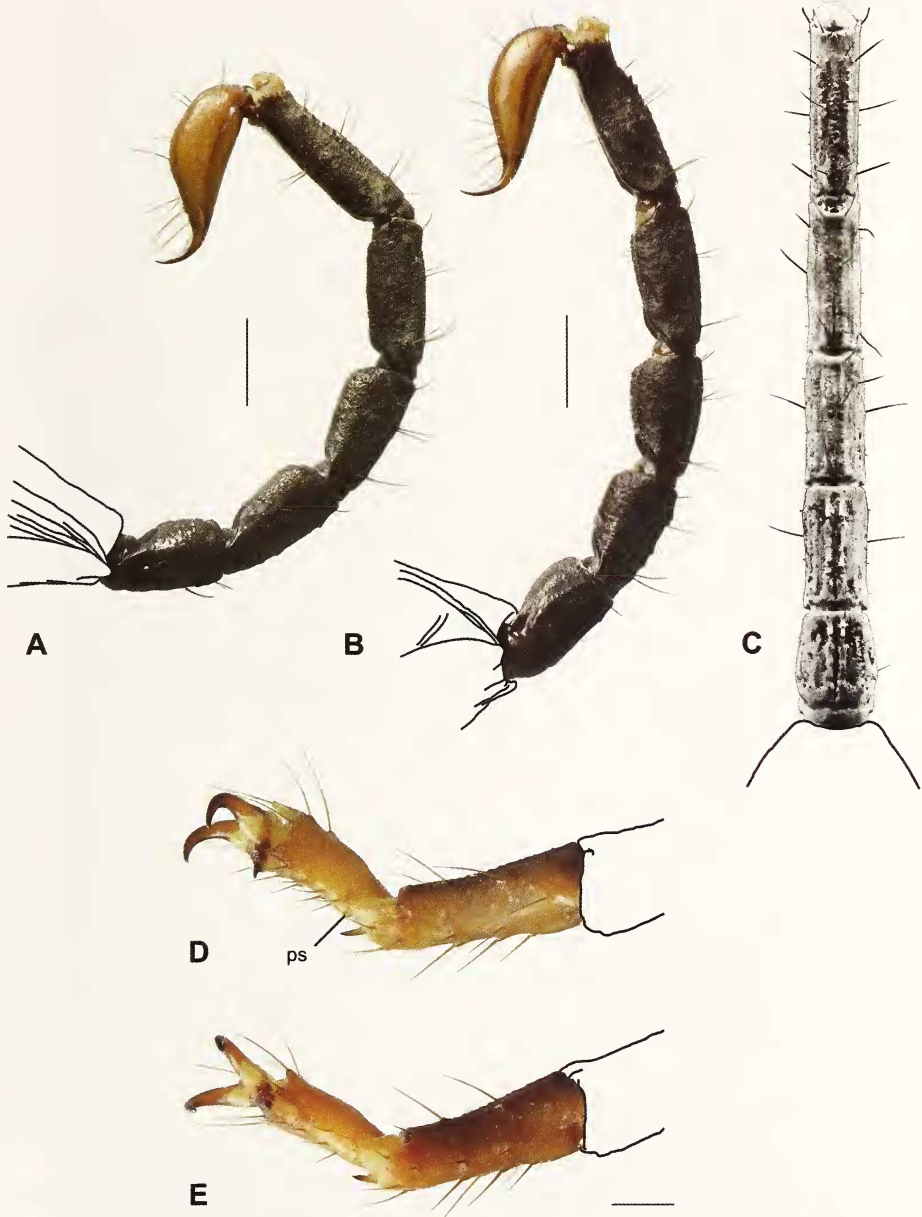


FIG. 28

Hormurus macrochela n. spec., metasoma and telson, lateral aspect (A, B) and ventral (C) aspect, and left tarsus IV, retrolateral (D) and ventral (E) aspect. (A) Paratype female (QM-S59206). (B-E) Holotype male (QM-S59212). Abbreviation: ps (proximal spinules). Scale, 3 mm (A, B), 1 mm (D, E).

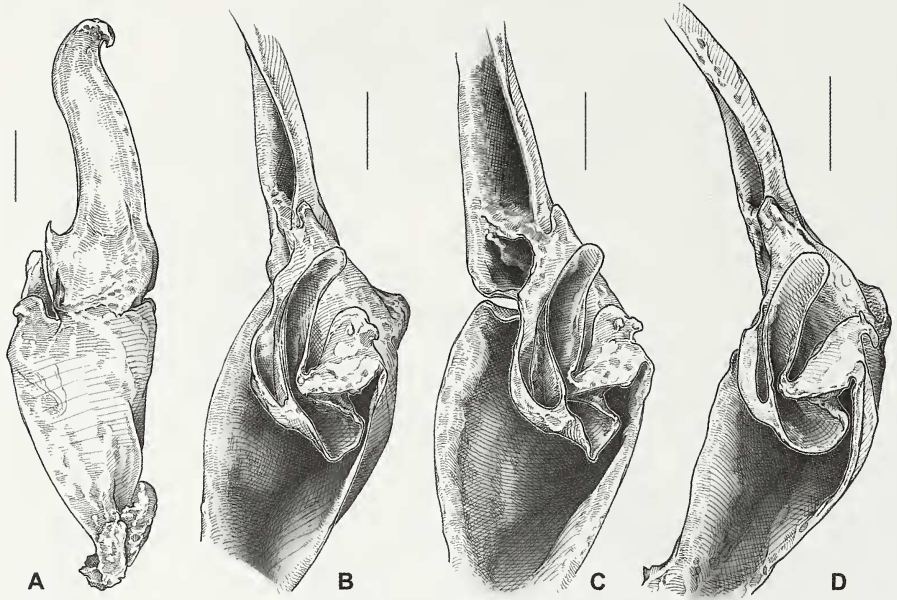


FIG. 29

Hormurus macrochela n. spec., holotype male (QM-S59212) (A-C), male from Magnetic Island (MHN) (D), left hemispermaphore. (A) Dorsal aspect. (B-D) Detail of capsular region, ental (B, D) and ventral (C) aspect. Scale, 1 mm.

Genital operculum: Composed of two subtriangular sclerites (Fig. 27A).

Pectines: Pectines slightly elongated, distal edge reaching but not surpassing distal edge of leg IV coxa (Fig. 27A); fulcra and three marginal lamellae present. Pectinal tooth count 7-9; teeth long and straight, entirely covered with sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth (Fig. 24A, E). Posterior margins of post-tergites I-VII sublinear, without distinct prominence (Fig. 24A, E); I-VI each with lateral transverse sulci; intercarinal surfaces of I-VII finely granular, at least in posterior half, more sparsely granular medially on I-III; intercarinal surfaces of III-VII uneven, with a distinct reticulated network of ridges and dimples. Respiratory stigmata (spiracles) of sternites IV-VI, short, less than one third sternite width and crescent-shaped, with distinct curve; sternite VII acarinate.

Metasoma: Length similar to that of ♀ (Tab. 3), not flattened laterally (Fig. 28B, C), intercarinal surfaces sparsely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae obsolete; dorsolateral, ventrolateral and ventro-submedian carinae distinct on at least some segments. Segment I: Width less than or equal to height (Tab. 3); dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carinae distinct; ventro-

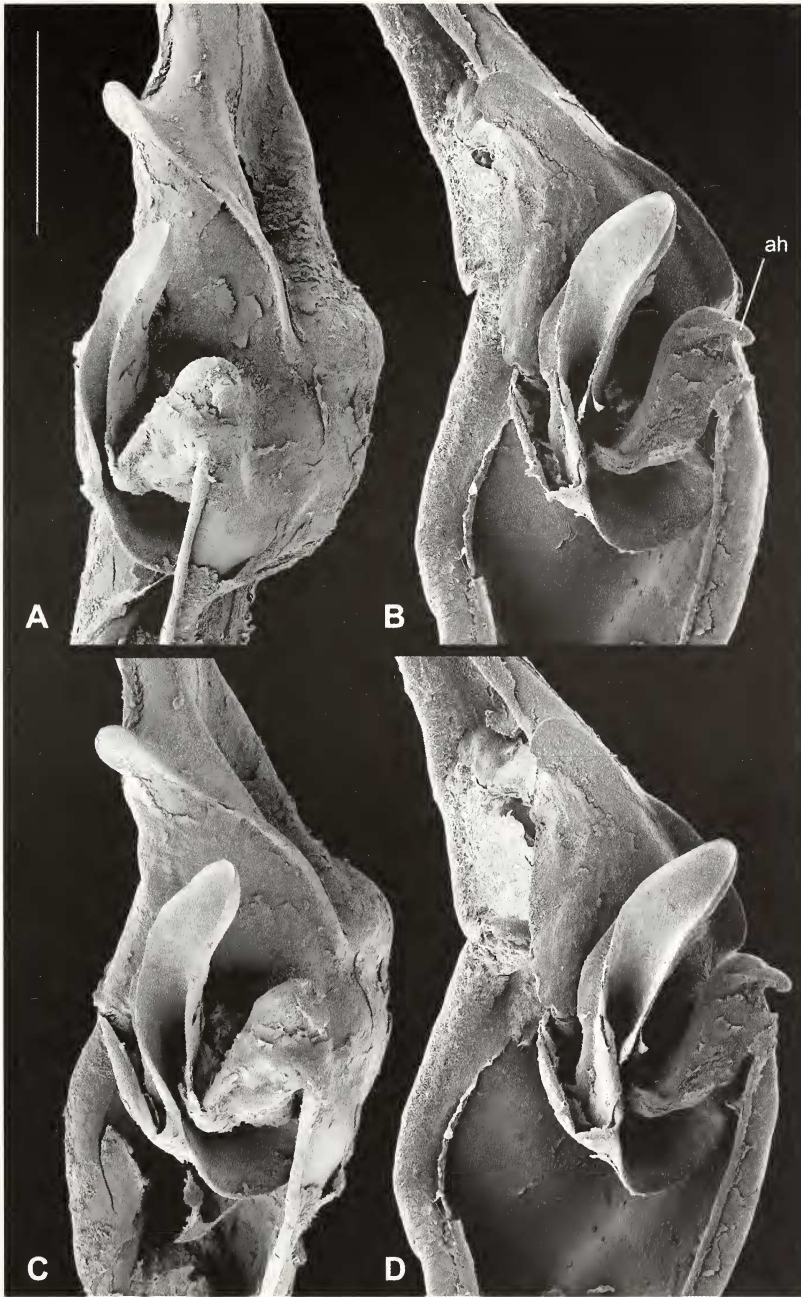


FIG. 30

Hormurus macrochela n. spec., male from Magnetic Island (MHN), left hemispermatophore, detail of capsular region. (A) Rotated approximately 30° clockwise from ental aspect. (B) Rotated approximately 30° counter-clockwise from ental aspect. (C) Ental aspect. (D) Ventral aspect. Abbreviation: ah (accessory hook). Scale, 1 mm.

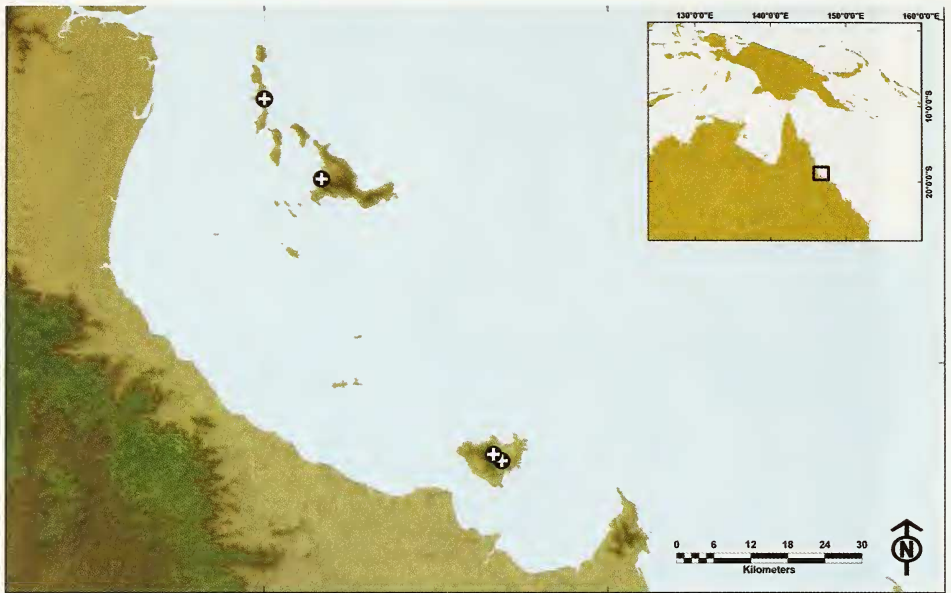


FIG. 31

Known localities of *Hormurus macrochela* n. spec. in northern Queensland, Australia, with topography indicated.

submedian carinae each with one or two spiniform granules subposteriorly, without spiniform granules medially or posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae without spiniform granules; ventro-submedian carinae each with one or two small spiniform granules medially, one or two subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral and ventro-submedian carinae weakly developed, sparsely granular, without spiniform granules. Segment V: Dorsal intercarinal surface sparsely granular; dorsolateral carinae obsolete; ventrolateral carinae weakly developed, posterior half comprising few spiniform granules becoming larger posteriorly; ventro-median carina weakly developed, comprising a sparse row of granules in anterior half, indistinct posteriorly; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 28B); vesicle surfaces smooth.

Hemispermatoaphore (Figs 29-30): Distal lamina gently curved, approximately same length as basal part; distal crest absent; single laminar hook situated in basal third; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded proximally and unfolded distally to a flattened extremity (tip and base approximately the same width); longitudinal carina on dorsal surface absent; accessory hook

and accessory lobe absent; lamellar tip situated proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory carina or crest, and with one or two large proximad-oriented accessory hooks on ental surface (Figs 29B-D, 30). Basal lobe well developed, spoon-shaped, merging with ental basal process; ectal edge without accessory fold, forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: All segments shorter and more robust than in male (Figs 23B, D, 25A, F, K, 26B). Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Fig. 26B).

Genital operculum: Oval to semi-oval, wider than long, approximately same width as sternum (Fig. 27B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of leg IV coxa (Fig. 27B). Pectinal tooth count 5-7; teeth short and curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-III smooth medially, granular laterally (Fig. 24B, F); intercarinal surfaces of IV-VI smooth or nearly so; intercarinal surfaces of VII granular posteriorly.

INTRASPECIFIC VARIATION: The pedipalps of larger males are proportionally longer than those of smaller males (positive allometry) (Monod, Harvey & Prendini, in preparation). Pectinal tooth counts vary from seven to nine in males and from five to seven in females. The distal lobe of the hemispermatophore usually bears one large hook on the ental edge, but two were observed in some specimens (Fig. 29A-C). This hook may be much more elongated, with a small posteriad-oriented excrescence (Fig. 29D) in some specimens.

REMARKS: Koch (1977) mentioned the large size of the pedipalp chela of specimens examined from Palm Island, but considered them conspecific with *L. waigiensis*. Volschenk *et al.* (2001) identified a specimen of this species from Magnetic Island as *L. waigiensis* based on the taxonomy current at the time.

DISTRIBUTION AND ECOLOGY: *Hormurus macrochela* is recorded from vine forests on three islands off the eastern coast of northern Queensland, between Ingham and Townsville (Fig. 31). Specimens were collected from narrow rock crevices and between stones near creeks in vine forest and rainforest. The habitat and habitus are consistent with the lithophilous ecomorphotype (Prendini, 2001).

CONSERVATION STATUS: The known populations of *H. macrochela* are situated on islands off the coast of northern Queensland, most of which are protected and part of two national parks (Orpheus Island National Park, Magnetic Island National Park). Therefore this species is not threatened by habitat destruction.

***Hormurus ochyroscapter* Monod, n. spec.**

Figs 32-37

Liocheles waigiensis: Koch, 1977 (misidentification, part): 169, 171, 172.

HOLOTYPE: QM-S17072; ♂; Australia, Queensland, Reedybrook [18°45'S, 144°38'E]; 2.VIII.1967; excavated from hole 6 inches deep, J. D. Brown.



FIG. 32

Hormurus ochyroscapter n. spec., male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

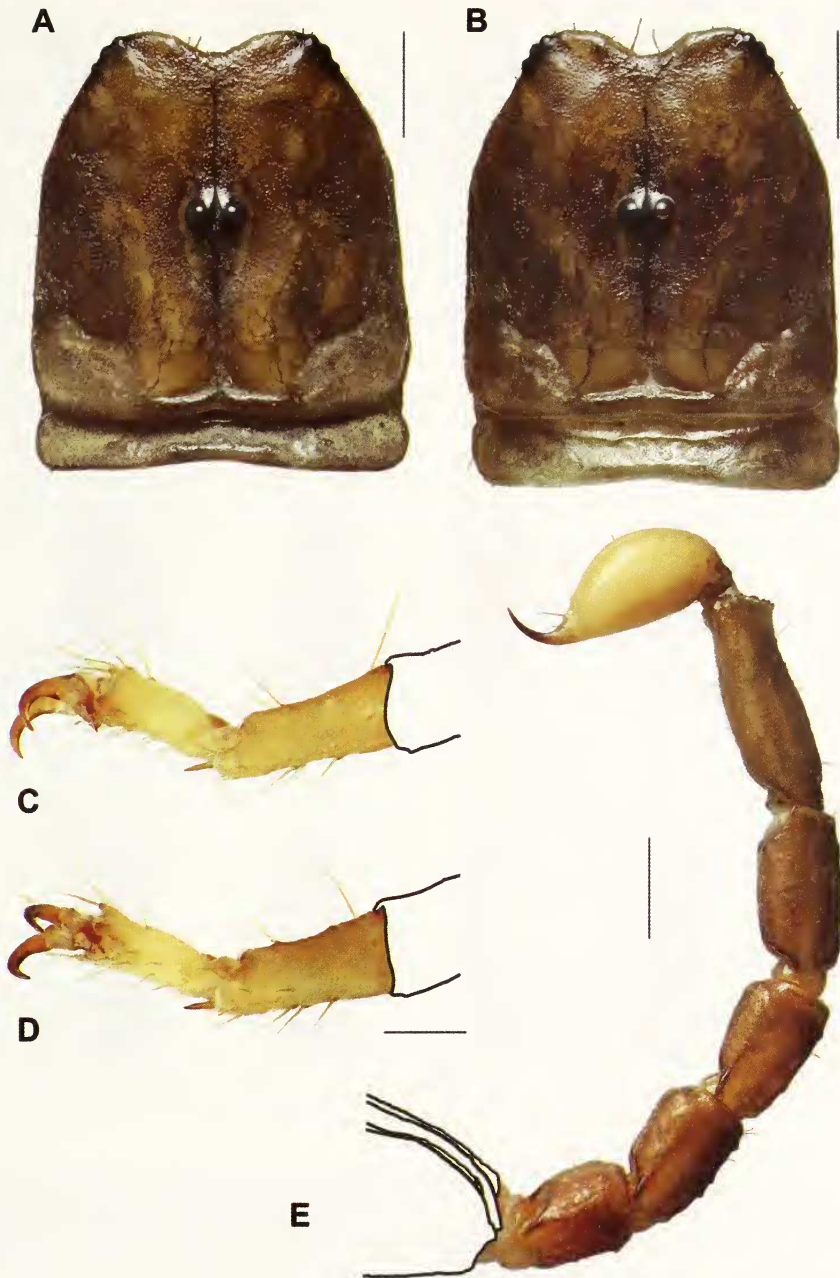


FIG. 33

Hormurus ochyroscaptor n. spec., carapace and mesosomal tergite I (A, B), left tarsus IV, retro-lateral (C) and ventral (D) aspect, and metasoma and telson, lateral aspect (E). (A, C-E) Holotype male (QM-S17072). (B) Paratype female (QM-S17072). Scales, 2 mm (A, B, E), 1 mm (C, D).

PARATYPES: QM-S17072; 1 ♀, 2 imm.; same data as holotype.

OTHER MATERIAL: AM KS94922; 1 imm.; Almaden [17°20'S, 144°41'E], Chillagoe District; XI-XII.1925; W. D. Campbell.

ETYMOLOGY: The name *ochyroscapter* is constructed from the Greek words *ochyros* [strong, stout] and *skapter* [digger]. It is an invariable noun in apposition and refers to the robust pedipalps of this species that are typical of fossorial hormurids.

DIAGNOSIS: *Hormurus ochyroscapter* differs from other Australian hormurids as follows. The pedipalps of *H. ochyroscapter* are short and robust unlike those of other Australian species, which are more elongate. The digital carina of the pedipalp chela manus is smooth (costate) and the internomedian carina obsolete in *H. ochyroscapter*, whereas in other species the digital carina is granular and the internomedian carina distinct and at least weakly granular. The patellar prolateral process is weakly developed in *H. ochyroscapter*, its two spiniform granules fused medially but not developed into a prominent median spine as in other species. Pedipalp patellar trichobothrium *esb*₂ is situated closer to trichobothria *em*₁ and *em*₂ than to trichobothrium *esb*₁ in *H. ochyroscapter*, whereas in other species it is situated closer to *esb*₁. One pair of subposterior spiniform granules and one pair of weak medial spiniform granules, present on the ventro-submedian carinae of metasomal segment III in *H. ochyroscapter*, are absent in other species.

MEASUREMENTS: Holotype male (QM-S17072): Total body length, 47.0. Carapace length, 6.8, anterior width, 4.8, posterior width, 7.0. Pedipalp chela length, 13.2, manus width, 4.5, manus height, 3.1; movable finger length, 6.4; patella length, 7.2, width, 3.1; femur length, 6.2, width, 2.8. Metasomal segment I length, 2.9, width, 1.9; segment V length, 4.3, width, 1.5, height, 1.4; telson vesicle width, 1.6, vesicle height, 1.9. Paratype female (QM-S17072): Carapace length, 6.7, anterior width, 4.9, posterior width, 6.7. Pedipalp chela length, 11.6, manus width, 4.6, manus height, 3.2; movable finger length, 5.8; patella length, 6.1, width, 3.0; femur length, 5.0, width, 2.4. Metasomal segment I length, 2.8, width, 1.8. (measurements for metasomal segment V and telson were not recorded because the specimen is damaged).

DESCRIPTION OF ADULT MALE: *Colouration*: Dorsal surface of chelicera manus yellow to pale brown; darker infuscations on fingers (Fig. 32). Carapace pale to dark brown. Pedipalps yellow to pale brown; carinae and fingers reddish brown to black. Legs pale yellow. Tergites pale to dark brown, slightly paler than carapace. Coxapophyses, sternum, genital operculum, pectines and sternites pale yellow. Metasoma yellow to pale brown. Telson yellow; aculeus reddish black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma, and metasoma finely punctate.

Carapace: Anterior margin with shallow median notch (Fig. 33A). Anterior furcated sutures and sulci distinct. Median ocular tubercle situated anteromedially, slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated by at least half the diameter of a median ocellus. Three pairs of lateral ocelli, equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces finely granular, at least sparsely so, except anteromedially, with frontal lobes smooth and fine granulation restricted to surfaces adjacent to anterior furcated and median longitudinal sulci.

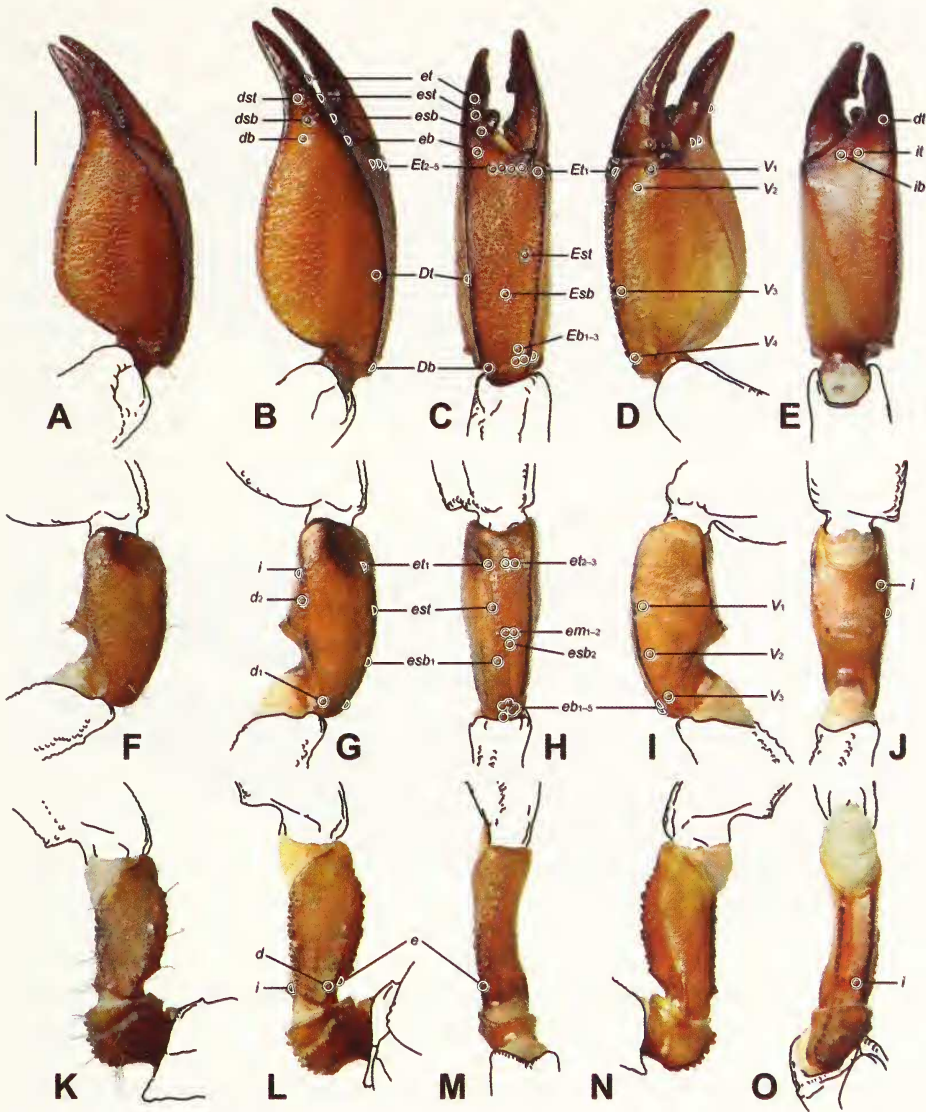


FIG. 34

Hormurus ochyroscapter n. spec., pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect, illustrating trichobothrial pattern. (A, F, K) Paratype female (QM-S17072). (B-E, G-J, L-O) Holotype male (QM-S17072). Scale, 2 mm.

Chelicerae: Median and basal teeth of fixed finger fused into a bicusp. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: All segments short and robust (Figs 32, 34B-E, G-J, L-O, 35A), with femur length less than carapace length. Chela almost asetose. Chela fingers: Dentate

margins of fixed and movable fingers linear (without lobes and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe well developed, conical; suprabasal notch distinct and deep (Fig. 35A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, wider than high, gently rounded dorsally and lacking a sharp conical tooth, not overlapping fixed finger; suprabasal lobe and corresponding suprabasal notch in fixed finger contiguous, no proximal gap or at most a reduced gap evident when fingers closed. Pedipalp carinae: Femur (Fig. 34L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal carina absent; internomedian ventral carina vestigial, comprising two large spiniform granules situated proximally and medially on segment; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 34G-J): Prolateral process distinct but weakly developed, comprising two distinct spiniform granules fused medially but not developed into a prominent median spine; internodorsal and dorsomedian carina distinct; dorsoexternal carina obsolete; externomedian carina costate-granular; ventroexternal carina distinct, costate. Chela manus (Fig. 34B-E): Dorsal secondary carina obsolete; digital carina distinct, costate, more strongly developed than external secondary carina; external secondary carina absent or obsolete; ventroexternal carina granular or crenulate; ventromedian and ventrointernal carinae obsolete; internomedian carina obsolete. Surface macrosculpture: Femur (Fig. 34L-O): Dorsal intercarinal surface densely granular except distally; retrolateral intercarinal surface at least sparsely granular dorsally, smooth or nearly so ventrally; ventral intercarinal surface granular proximally, smooth distally; prolateral intercarinal surface smooth except for a sparsely granular zone proximally. Patella (Fig. 34G-J): Dorsal and retrolateral intercarinal surfaces granular or at least comprising a reticulated network of granules; ventral intercarinal surface sparsely granular, distal extremity smooth; prolateral intercarinal surface sparsely granular proximally, smooth or nearly so in distal half. Chela (Fig. 34B-E): Dorsal and retrolateral intercarinal surfaces of manus densely granular, comprising medium-sized granules; ventral intercarinal surface granular along pro- and retrolateral margins only, smooth medially; prolateral intercarinal surface sparsely granular, less so along ventral margin. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). Trichobothria: Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 34B-E, G-J, L-O). Patella: d_2 distal to patellar process; five *eb* trichobothria arranged in two groups, eb_1 and eb_{2-5} ; two *esb* trichobothria; two *em* trichobothria; *esb-em* series arranged in two groups, esb_2 and esb_1/em_{1-2} ; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated in proximal third; Eb_3 situated close to Eb_{1-2} ; *Esb* situated midway between *Eb* series and *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with V_3 and V_4 separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

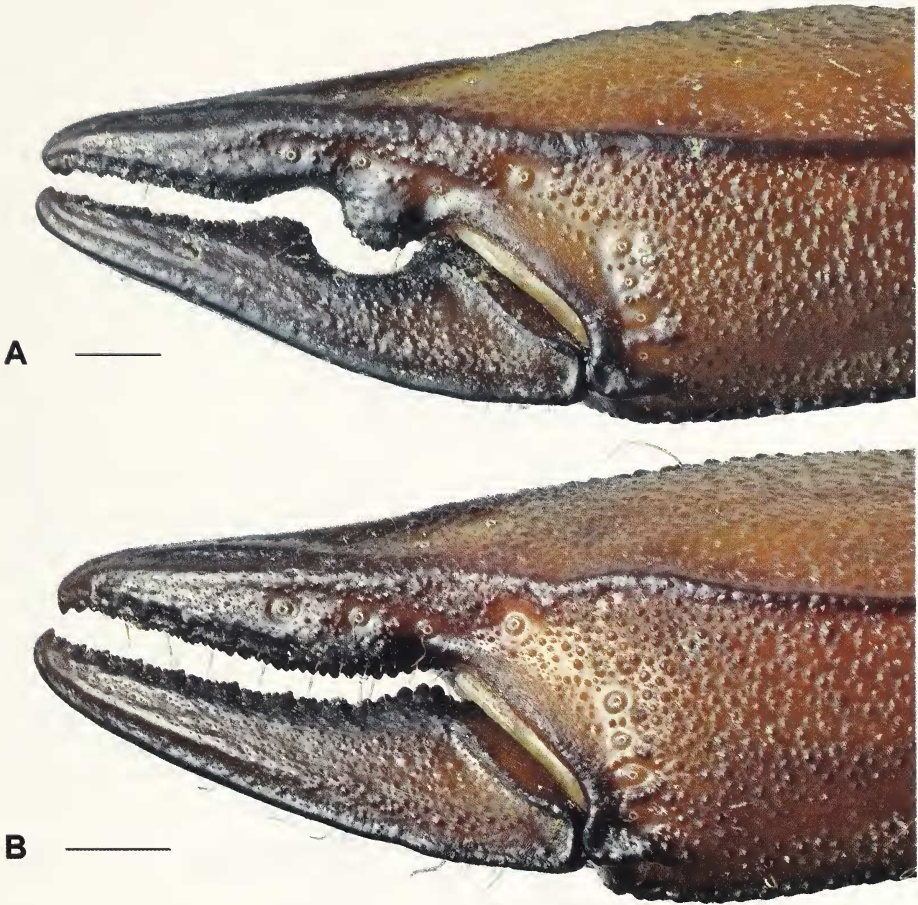


FIG. 35

Hormurus ochyroscapter n. spec., pedipalp chela, retrolateral aspect illustrating dentate margin of chela fingers. (A) Holotype male (QM-S17072). (B) Paratype female (QM-S17072). Scale, 1 mm.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 36A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 4-5/5 and 5/5 setiform macrosetae, respectively (Fig. 33C, D); ventromedian row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; ungues curved, shorter than telotarsus.

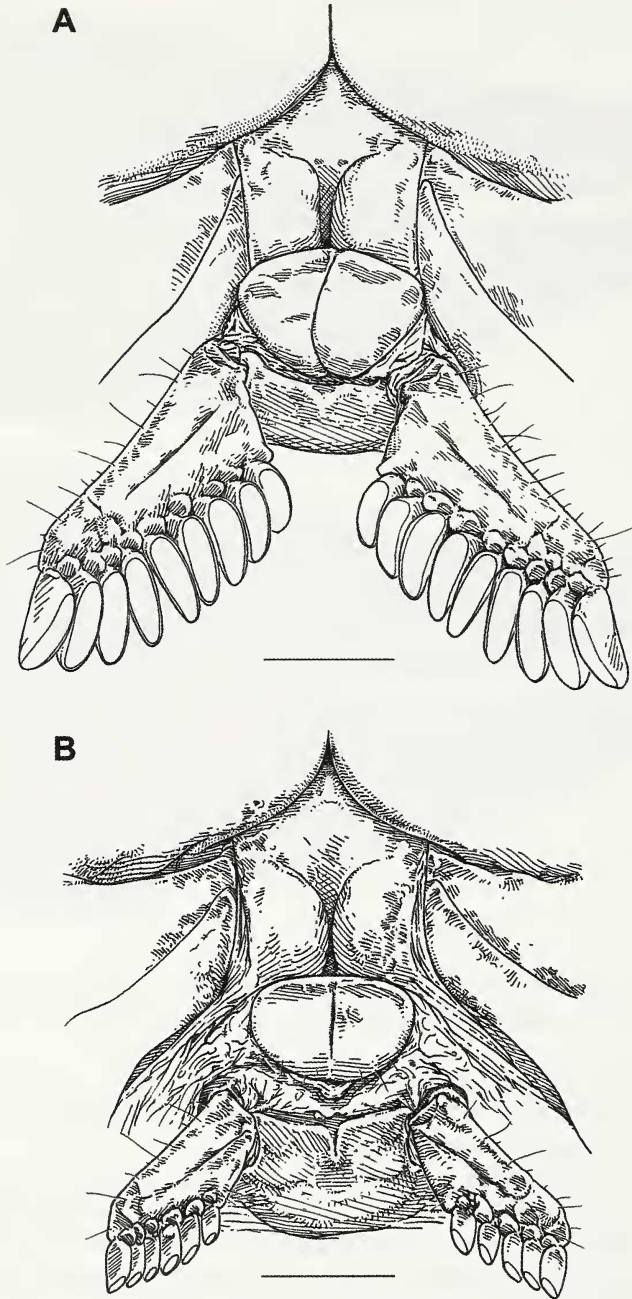


FIG. 36

Hormurus ochyroscapter n. spec., coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Holotype male (QM-S17072). (B) Paratype female (QM-S17072). Scale, 1.5 mm.

Genital operculum: Composed of two subtriangular sclerites (Fig. 36A).

Pectines: Slightly elongated, distal edge reaching and surpassing distal edge of leg IV coxa (Fig. 36A); fulcra and three marginal lamellae present. Pectinal tooth count 8-9; teeth, long, straight, entirely covered with sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth. Posterior margins of post-tergites I-VII sublinear, without distinct prominence; I-VI each with lateral transverse sulci; intercarinal surfaces of I-VII finely granular, at least sparsely so in posterior half; intercarinal surfaces of III-VII uneven, with a distinct reticulated network of ridges and dimples. Respiratory stigmata (spiracles) of sternites IV-VI short, less than one third sternite width and crescent-shaped, with distinct curve; sternite VII acarinate.

Metasoma: Length similar to that of ♀, not flattened laterally (Fig. 33E), intercarinal surfaces sparsely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae absent or obsolete on all segments; dorsolateral, ventrolateral and ventro-submedian carinae distinct on at least some segments. Segment I: Width less than or equal to height; dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carina distinct; ventro-submedian carinae each with one or two weakly developed spiniform granules medially, one or two subposteriorly, and none posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae without spiniform granules; ventro-submedian carinae each with one or two spiniform granules medially, 1-3 subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae weakly developed, comprising a sparse row of granules, without larger spiniform granules; ventro-submedian carinae weakly developed, each with one weakly developed spiniform granule medially and one subposteriorly on III, and with several larger spiniform granules posteriorly on IV. Segment V: Dorsal intercarinal surface sparsely granular; dorsolateral carinae obsolete; ventrolateral carinae indistinct in anterior half, comprising few medium-sized spiniform granules in posterior half; ventromedian carina weakly developed, indistinct posteriorly; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 33E); vesicle surfaces smooth.

Hemispermaphore: Distal lamina gently curved, slightly longer than basal part; distal crest absent; single laminar hook situated in basal third; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded proximally and unfolded distally to a flattened extremity (tip and base approximately the same width); longitudinal carina on dorsal surface absent to weak; accessory hook and accessory lobe absent; lamellar tip situated slightly proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory



FIG. 37

Known localities of *Hormurs ochyroscapter* n. spec. in northern Queensland, Australia, with topography indicated.

carinae or crest, and with small proximad-oriented accessory hook on ental surface. Basal lobe well developed, spoon-shaped, merging with ental accessory lobe; ectal edge without accessory fold (no groove), forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Figs 34A, F, K, 35B).

Carapace: Medial surfaces slightly less granular than in male (Fig. 33B).

Genital operculum: Oval to semi-oval, wider than long, approximately same width as sternum (Fig. 36B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of leg IV coxa (Fig. 36B). Pectinal tooth count 5-7; teeth short, curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-VII smooth or nearly so; intercarinal surfaces of III-VII even, reticulated network of ridges and dimples absent or obsolete.

INTRASPECIFIC VARIATION: Pectinal tooth counts vary from eight to nine in males, and from five to seven in females.

REMARKS: Koch (1977) mentioned the short pedipalps and unusual shape of the patellar process of specimens from Almaden and Reedybrook (constituting the examined material of *H. ochyroscapter*), but considered them conspecific with *L.*

waigiensis. Only one adult male and one adult female are known. Both are severely damaged, hence certain characters (female habitus, carapace and tergite macrosculptures, metasoma of female, hemispermatophore) are not illustrated.

DISTRIBUTION: *Hormurus ochyroscapter* is recorded from open woodlands and savannah in the Charter Towers region and the Shire of Etheridge in Far North Queensland (Fig. 37).

ECOLOGY: *Hormurus ochyroscapter* was collected close to a waterbody in an inland savannah, a habitat similar to that of *H. ischnoryctes*. However, the climate at the type locality of *H. ochyroscapter* is drier than at the type locality of *H. ischnoryctes*, and there are no major rock formations that could potentially sustain humid conditions for extended periods. The known specimens of this fossorial species were excavated from ca 15 cm deep burrows. The habitat and habitus are consistent with the pelophilous ecomorphotype (Prendini, 2001).

CONSERVATION STATUS: This species is known from only two localities situated within the boundaries of privately owned cattle stations. The type specimens were collected in 1967 and no other specimens have been collected since. The first author visited Reedybrook in 2006 to obtain more specimens, but failed to find any during several days of intensive searching. The habitat there was severely disturbed by livestock, and this population of *H. ochyroscapter* may be extinct. Although there are no empirical data, it appears that population densities of burrowing scorpions in different parts of the world decline in areas where large numbers of hooved livestock are maintained, perhaps because their burrows are continuously damaged by the trampling of hooves, or due to a decrease in prey abundance and/or humidity associated with overgrazing of the vegetation (L. Monod and L. Prendini, personal observations). Based on the restricted distribution and degradation of its habitat, and despite the scarcity of data available on its distribution, ecology and abundance, it is recommended that *H. ochyroscapter* be placed on the IUCN Red List of endangered species (IUCN, 2001).

DISCUSSION

Most fossorial hormurid species belong to the genus *Cheloctonus* Pocock, 1892 from the semi-arid savannas of southern Africa. Several species of this genus construct vertical burrows with terminal chambers in open ground or against the sides of stones, in soils with high clay content, e.g. black turf (Newlands, 1972, 1978; Harington, 1978; Prendini, 2001, 2005b). Burrow entrances are slit-like in shape, and wider than high. Population densities of up to four individuals per square metre have been recorded for *Cheloctonus jonesii* Pocock, 1892 (Harington, 1978; L. Prendini, personal observation). Burrows of this species are 15-30 cm deep, with entrances 2-3 cm by 1-1.5 cm, and a small heap of excavated stones and soil particles is often present on one or both sides (Harington, 1978). The term 'spoil' is used in the present paper to designate these debris mounts instead of 'tumulus' originally proposed by Williams (1966). A spoil refers to the material (earth and rocks) removed during an excavation and is thus a more appropriate name than tumulus which refers to a mound of earth and stones raised over a grave.

Similar burrow architecture and population densities were observed for two species of *Liocheles* from Asia. In the woodlands and forests of India, *Liocheles*

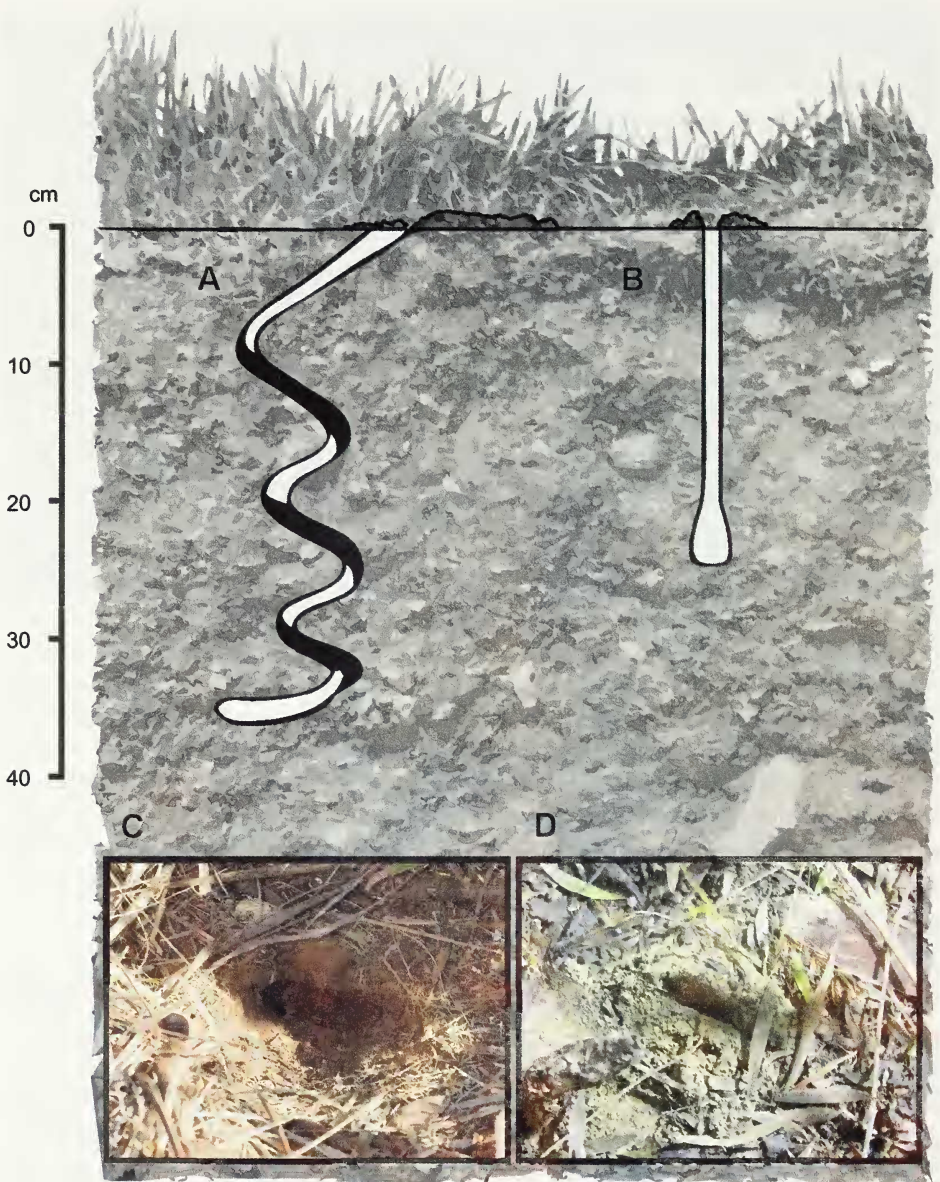


FIG. 38

Burrow architecture in urodacid and hormurid scorpions. (A) *Urodacus yaschenkoii* (Birula, 1903), diagrammatic cross-section of burrow (adapted from <http://www.thedailylink.com/thespiralburrow/>). (B) *Hormurus ischnoryctes* n. spec., diagrammatic cross-section of burrow. (C) *Urodacus* sp. from Mitchell River National Park, Western Australia, burrow entrance. (D) *Hormurus ischnoryctes* n. spec., burrow entrance. Scale in cm.

nigripes reportedly excavates vertical burrows 40-60 cm deep in sandy and stony soils with entrances 1.5-2.5 cm by 0.4-0.6 cm (Tilak, 1970). An undetermined fossorial *Liocheles* was recently collected in a Vietnamese forest (under closed canopy) by L. Prendini. The vertical burrows of this species were approximately 10 cm deep, and were constructed in open ground or along the side of a stone, along an earthen embankment comprising sandy-clay soil (L. Prendini, personal observation). A spoil was observed on one or both sides of the silt-like entrances, which were about 1 cm by 0.5 cm.

The burrows of *H. ischnoryctes* from the savanna of Queensland are vertical and about 15-30 cm deep, with a slit-like entrance and an enlarged terminal chamber (L. Monod, personal observation, Fig. 38B, D), much like in *C. jonesii*. The density of burrows in the only known population of this species appeared comparable to those of *C. jonesii* and *L. nigripes*, with numerous entrances in a small area. Burrows were predominantly located at the bases of trees and shrubs. Observations were made after unusually heavy rainfalls during the dry season. Most of the burrow entrances had recently excavated spoils on the sides, i. e. soil presumably carried outside the burrows by the scorpions after the rains subsided, as reported for *C. jonesii* (Harington, 1978).

According to the data labels, the known specimens of *H. ochyroscapter* were excavated from burrows approximately 15 cm deep. Unfortunately no other data concerning the burrow entrance or density are available for this species.

Burrowing behaviour appears to have evolved independently in three genera of Hormuridae, i.e. *Cheloctonus*, *Hormurus* and *Liocheles*. *Cheloctonus* is placed basal in the phylogeny of Hormuridae, and does not form a monophyletic group with *Hormurus* and *Liocheles* (Prendini, 2000). Additionally, *L. nigripes* does not form a monophyletic group with the two fossorial species of *Hormurus* (Monod, 2011; Monod & Prendini, in preparation), and it is presently unknown whether *H. ischnoryctes* and *H. ochyroscapter* are sister species. If the two fossorial *Hormurus* are not monophyletic, burrowing behaviour would have evolved independently on four occasions within the family.

Although there is no common ancestry for burrowing behaviour in Hormuridae, the burrow architecture is remarkably similar in all hormurid species in which it has been observed, suggesting a parallel evolution (sensu Powell, 2007). Moreover, burrow architecture is quite different in fossorial species of the closely related scorpionoid families Diplocentridae Karsch, 1880, Scorpionidae Latreille, 1802 and Urodacidae Pocock, 1893, the more distantly related Bothriuridae Simon, 1880, and the chactoid genera *Anuroctonus* Pocock, 1893 and *Hadrurus* Thorell, 1876. Most species in these taxa construct burrows at a 5-50° angle to the ground surface, rather than vertically, and often spiral down to an enlarged terminal chamber (Fig. 38A; Williams, 1966; Koch, 1978; Lamoral, 1979; Shorthouse & Marples, 1980; Shivashankar, 1992, 1994; Prendini *et al.*, 2003; Hembree *et al.*, 2012; L. Prendini, personal observation). The difference in burrow architecture is probably a consequence of the difference in the mechanics of burrow excavation. Fossorial hormurids are pedipalp burrowers that use the large, often rounded pedipalpal chelae to loosen the soil and carry it out of the burrow, whereas the other taxa are cheliceral burrowers that use their enlarged chelicerae to loosen the soil and then scrape it out of the burrow using the legs and/or

metasoma (Newlands, 1972; Eastwood, 1978; Harington, 1978; Prendini, 2001, 2005b; Hembree *et al.*, 2012).

Blackledge & Gillespie (2004) demonstrated that similar web architectures, termed “ethotypes”, evolved independently in species of *Tetragnatha* Latreille, 1804 spiders from different Hawaiian islands, illustrating the high level of predictability that evolutionary diversification of complex behaviours may exhibit. Although less elaborate than web construction, burrow excavation is nonetheless a complex task, costly in time and energy (Shorthouse, 1971; Shorthouse & Marple, 1980; White, 2001), the expression of which appears to follow fixed patterns much like web construction in spiders. These observations in turn suggest that genetic pathways of burrowing behaviour, although not expressed, are conserved in hormurids that are not fossorial. Similar burrow architecture among distantly related hormurid genera suggests that burrowing behaviour did not evolve *de novo* in derived hormurid species, but is rather the expression of a basic behavioural trait suppressed in the common ancestor of Hormuridae. The suppression and re-expression of complex morphological structures or behaviours in distantly related lineages appears to be a more general trend than previously recognized (Wilkinson & Dodson, 1997; Whiting *et al.*, 2003; Bonduriansky, 2006) and points to the synergistic effect of similar selection pressures on highly conserved genetic pathways as a general mechanism for convergent evolution (Osorio & Bacon, 1994; Reichert & Boyan, 1997; Tomarev *et al.*, 1997; Ogura *et al.*, 2004; Emlen *et al.*, 2005).

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REFERENCES

- BANFAI, D. S. & BOWMAN, D. M. J. S. 2006. Forty years of lowland monsoon rainforest expansion in Kakadu National Park, Northern Australia. *Biological Conservation* 131: 553-565.
- BECKER, J. J., SANDWELL, D. T., SMITH, W. H. F., BRAUD, J., BINDER, B., DEPNER, J., FABRE, D., FACTOR, J., INGALLS, S., KIM, S.-H., LADNER, R., MARKS, K., NELSON, S., PHARAOH, A., TRIMMER, R., VON ROSENBERG, J., WALLACE, G. & WEATHERALL, P. 2009. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy* 32: 355-371. Available at http://topex.ucsd.edu/WWW_html/srtm30_plus.html (accessed 2011).
- BIRULA, A. A. 1903. Sur un nouveau genre et une nouvelle espèce de scorpion provenant d'Australie. *Annales du Musée Zoologique de l'Académie Impériale des Sciences de St-Petersbourg, Nouvelles* 8: 33 [in Russian, diagnosis in Latin].
- BLACKLEDGE, T. A. & GILLESPIE, R. G. 2004. Convergent evolution of behaviour in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences* 101(46): 16228-16233.
- BONDURIANSKY, R. 2006. Convergent evolution of sexual shape dimorphism in Diptera. *Journal of Morphology* 267: 602-611.
- BOWMAN, D. M. J. S., WILSON, B. A. & MACDONOUGH, L. 1991. Monsoon forests in north-western Australia. I. Vegetation classification and the environmental control of tree species. *Journal of Biogeography* 18: 679-686.
- BULTITUDE, R. J., GARRAD, P. D., DONCHAK, P. J. T., DOMAGALA, J., CHAMPION, D. C., REES, I. D., MACKENZIE, D. E., WELLMAN, P., KNUSTON, J., FANNING, C. M., FORDHAM, B. G., GRIMES, K. G., OVERSBY, B. S., RIENKS, I. P., STEPHENSON, P. J., CHAPPELL, B. W., PAIN, C. F., WILFORD, J. R., RIGBY, J. F. & WOODBURY, M. J. 1997. Chapter 7. Cairns region. (pp. 225-325). In: BAIN, J. H. C. & DRAPER, J. J. (eds). North Queensland geology. *Australian Geological Survey Organisation Bulletin 240 / Queensland Department of Mines and Energy Queensland Geology* 9, 600 pp.
- CHAPMAN, A. D. & GRAFTON, O. 2008. Guide to best practices for generalising primary species-occurrence data, version 1.0. *Global Biodiversity Information Facility, Copenhagen*, 27 pp. Available at <http://www2.gbif.org/BPsensitivedata.pdf> (accessed 2011).
- COUZIEN, H. W. C. 1976. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. *Netherlands Journal of Zoology* 26: 453-501.
- EASTWOOD, E. B. 1978. Notes on the scorpion fauna of the Cape. Part 4. The burrowing activities of some scorpionids and buthids (Arachnida, Scorpionida). *Annals of the South African Museum* 74: 249-255.
- EMERSON, D. W., MILLS, K. J., MIYAKAWA, K., HALLETT, M. S. & CAO, L. Q. 1992. Alligator Rivers Region Analogue Project, Final Report. Volume 4. Geophysics, petrophysics and structure. *Australian Nuclear Science and Technology Organisation (ANSTO), Sydney*, 125 pp.
- EMLÉN, D. J., HUNT, J. & SIMMONS, L. W. 2005. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. *American Naturalist* 166: 42-68.
- FAGE, L. 1933. Les scorpions de l'Indochine française, leur affinités, leur distribution géographique. *Annales de la Société entomologique de France (Paris)* 102: 25-34.
- FET, V. 2000. Family Ischnuridae Simon, 1879 (pp. 383-408). In: FET, V., SISSOM, W. D., LOWE, G. & BRAUNWALDER, M. E. (eds). Catalog of the scorpions of the world (1758-1998). *New York Entomological Society, New York*, 690 pp.

- FORDYCE, I. R., DUFF, G. A. & EAMUS, D. 1997. The water relations of *Allosyncarpia ternata* (Myrtaceae) at contrasting sites in the monsoonal tropics of northern Australia. *Australian Journal of Botany* 45: 259-274.
- GALLOWAY, R. W. 1976. Geomorphology of the Alligator rivers area (pp. 52-70). In: STORY, R., GALLOWAY, R. W., MCALPINE, J. R., ALDRICK, J. M. & WILLIAMS, M. A. J. (eds). Lands of the Alligator Rivers Area, Northern Territory. *Land Research Series 38. CSIRO, Melbourne*, 171 pp.
- GERVAIS, P. 1843. Les principaux résultats d'un travail sur la famille des scorpions. *Société Philomatique de Paris. Extraits des Procès-Verbaux des Séances* 5(7): 129-131.
- HADLEY, A. 2005. CombineZM. Available at <http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm>.
- HADLEY, A. 2009. CombineZP. Available at <http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm>.
- HARINGTON, A. 1978. Burrowing biology of the scorpion *Cheloctonus jonesii* Pocock (Scorpionida, Scorpionidae). *Journal of Arachnology* 5: 243-249.
- HEMBREE, D. I., JOHNSON, L. M. & TENWALDE, R. W. 2012. Neoichnology of the desert scorpion *Hadrurus arizonensis*: burrows to biogenic cross lamination. *Palaeontologica Electronica* 15(1): 10A, 34 pp.
- HOATSON, D., BLAKE, D., WYGRALAK, A., NEEDHAM, S., ALLEN, B., MILES, G., HAUSER, P. & OSWALD-JACOBS, I. 2000. Birth of Kakadu and Nitmiluk (pp. 31-43). In: HOATSON, D., BLAKE, D., WYGRALAK, A., NEEDHAM, S., ALLEN, B., MILES, G., HAUSER, P. & OSWALD-JACOBS, I. (eds). Kakadu and Nitmiluk National Parks, Northern Territory. A guide to the rocks, landforms, plants, animals, Aboriginal culture, and human impact. *Australian Geological Survey Organisation, Canberra*, 110 pp.
- HUXLEY, T. H. 1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London* 36(1): 294-319.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN) 1999. International Code of Zoological Nomenclature - 4th Edition - *The International Trust for Zoological Nomenclature, The Natural History Museum, London*, 306 pp.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN) 2001. IUCN Red List categories and criteria. Version 3.1. IUCN *Species Survival Commission, IUCN, Gland, Switzerland / Cambridge, UK*. Available at http://www.iucnredlist.org/static/categories_criteria.
- JARVIS, A., REUTER, H. I., NELSON, A. & GUEVARA, E. 2008. Hole-filled seamless SRTM data V4. *International Centre for Tropical Agriculture (CIAT)*. Available at <http://srtm.csi.cgiar.org> (accessed 2011).
- JOHNSON, D. 2004. The geology of Australia. *Cambridge University Press, Cambridge*, 276 pp.
- KARSCH, F. 1880. Arachnologische Blätter. X. Scorpionologische Fragmente. *Zeitschrift für die Gesellschaft der Naturwissenschaften* 53: 404-409.
- KOCH, L. E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum* 5(2): 83-367.
- KOCH, L. E. 1978. A comparative study of the structure, function and adaptation to different habitats of burrows in the scorpion genus *Urodacus* (Scorpionida, Scorpionidae). *Records of the Western Australian Museum* 6(2): 119-146.
- KOVAŘÍK, F. 1998. Štíři (Scorpions). *Nakladatelství Madagaskar, Jihlava*, 175 pp.
- LAMORAL, B. H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23(3): 497-784.
- LATREILLE, P. A. 1802. Scorpionides (pp. 46-47). In: Histoire naturelle, générale et particulière, des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc et Buffon, et rédigée par C. S. Sonnini. Tome III. *Imprimerie F. Dufart, Paris*, 467 pp.
- LATREILLE, P. A. 1804. Tableau méthodique des insectes. *Nouveau Dictionnaire d'Histoire Naturelle, Paris* 21: 129-295.
- LAURIE, M. 1896. Further notes on the anatomy and development of scorpions, and their bearing on the classification of the order. *Annals and Magazine of Natural History* (6) 18: 9-133.

- LAWRENCE, R. F. 1954. Fluorescence in Arthropoda. *Journal of the Entomological Society of South Africa* 17: 167-170.
- LOCKET, A. 1995. A new ischnurid scorpion from the Northern Territory, Australia. *Records of the Western Australian Museum* supplement 52: 191-198.
- LOCKET, A. 1997. *Liocheles extensa*, a replacement name for *Liocheles longimanus* Locket, 1995 (Scorpiones: Ischnuridae). *Records of the Western Australian Museum* 18: 331.
- MONOD, L. 2000. Révision systématique du genre *Liocheles* (Ischnuridae, Scorpiones). *M.Sc. thesis, University of Geneva, Switzerland*, 143 pp.
- MONOD, L. 2011. The Liochelidae Fet & Bechly, 2001 (Scorpiones) of the Indo-Pacific region: Systematics and biogeography. *Ph.D. thesis, City University of New York*, 2 volumes, 848 pp.
- MONOD, L. & VOLSCHENK, E. S. 2004. *Liocheles litodactylus* (Scorpiones: Liochelidae): An unusual new *Liocheles* species from the Australian Wet Tropics (Queensland). *Memoirs of the Queensland Museum* 49(2): 675-690.
- MONTREAL PROCESS IMPLEMENTATION GROUP FOR AUSTRALIA (MPIGA) 2008. Australia's state of the forests report 2008. *Bureau of Rural Sciences, Canberra*, 250 pp.
- NAVIDPOUR, S. & LOWE, G. 2009. Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae). *Journal of Arachnology* 37: 45-59.
- NEWLANDS, G. 1972. Ecological adaptations of Kruger National Park scorpionids (Arachnida: Scorpiones). *Koedoe* 15: 37-48.
- NEWLANDS, G. 1978. Arachnida (except Acari) (pp. 677-684). In: WERGER, M. J. A. (ed.). *Biogeography and Ecology of southern Africa, volume 2. W. Junk, The Hague*, 777 pp.
- NOWAK, A., LIS, P. & RADZIEJEWSKA, T. 2008. Sonication as an aid in cleaning cladoceran remains extracted from sediment cores. *Journal of Paleolimnology* 39: 133-136.
- OGURA, A., IKEO, K. & GOJOBORI, T. 2004. Comparative analysis of gene expression for convergent evolution of camera eye between octopus and human. *Genome Research* 14: 1555-1561.
- OJANGUREN-AFFILASTRO, A. A., AGUSTO, P., PIZARRO-ARAYA, J. & MATTONI, C. I. 2007. Two new scorpion species of the genus *Brachistosternus* (Scorpiones: Bothriuridae) from northern Chile. *Zootaxa* 1623: 55-68.
- OJANGUREN-AFFILASTRO, A. A., FERNÁNDEZ CAMPÓN, F., LAGOS SILNIK, S. & MATTONI, C. I. 2009. The genus *Orobothriurus* Maury in central Argentina with description of a new species from El Nevado mountain chain in Mendoza Province (Scorpiones: Bothriuridae). *Zootaxa* 2209: 28-42.
- OSORIO, D. & BACON, J. P. 1994. A good eye for arthropod evolution. *Bioessays* 16: 419-424.
- PAVAN, M. 1954a. Presenza e distribuzione di una sostanza fluorescente nel tegumento degli scorpioni. *Bolletino della Società Italiana di Biologia Sperimentale* 30: 801-803.
- PAVAN, M. 1954b. Primi dati per la caratterizzazione della sostanza fluorescente nel tegumento degli scorpioni. *Bolletino della Società Italiana di Biologia Sperimentale* 30: 803-805.
- PAVAN, M. 1954c. Studi sugli scorpioni. I. Una nuova caratteristica tipica del tegumento degli scorpioni. *Italian Journal of Zoology* 21: 283-291.
- PAVAN, M. & VACHON, M. 1954. Sur l'existence d'une substance fluorescente dans les téguments de scorpions (Arachnides). *Comptes Rendus de l'Académie des Sciences (Paris)* 239: 1700-1702.
- POCOCK, R. I. 1892. Description of two new genera of scorpions, with notes on some species of *Palamneus*. *Annals and Magazine of Natural History* (6) 9: 38-49.
- POCOCK, R. I. 1893. Notes on the classification of scorpions, followed by some observations on synonymy, with descriptions of new genera and species. *Annals and Magazine of Natural History* (6) 12: 303-330.
- POCOCK, R. I. 1897. Description of some new species of scorpions from India. *Journal of the Bombay Natural History Society* 11: 102-117.
- POWELL, R. 2007. Is convergence more than an analogy? Homoplasy and its implications for macroevolution predictability. *Biology and Philosophy* 22: 565-578.

- PRENDINI, L. 2000. Phylogeny and classification of the superfamily Scorpionioidea Latreille, 1802 (Chelicerata, Scorpiones): an exemplar approach. *Cladistics* 16: 1-78.
- PRENDINI, L. 2001. Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited (pp. 113-138). In: FET, V. & SELDEN, P. A. (eds). *Scorpions 2001. In memoriam Gary A. Polis. British Arachnological Society, Burnham Beeches, Bucks*, 404 pp.
- PRENDINI, L. 2003a. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. *Systematic Entomology* 28: 149-172.
- PRENDINI, L. 2003b. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). *American Museum Novitates* 3408: 1-24.
- PRENDINI, L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): Revisions to the taxonomy and key to the species. *Journal of Arachnology* 32: 109-186.
- PRENDINI, L. 2005a. On *Hadogenes angolensis* Lourenço, 1999 syn. n. (Scorpiones, Liochelidae), with a redescription of *H. taeniurus* (Thorell, 1876). *Revue suisse de Zoologie* 112(2): 371-399.
- PRENDINI, L. 2005b. Scorpion diversity and distribution in southern Africa: Pattern and process (pp. 25-68). In: HUBER, B. A., SINCLAIR, B. J. & LAMPE, K.-H. (eds). *African Bio-diversity: molecules, organisms, ecosystems. Proceedings of the 5th International Symposium on Tropical Biology; Museum Alexander Koenig, Bonn; Springer Verlag, New York*, 443 pp.
- PRENDINI, L. 2006. New South African flat rock scorpions (Liochelidae: *Hadogenes*). *American Museum Novitates* 3502: 1-32.
- PRENDINI, L., CROWE, T. M. & WHEELER, W. C. 2003. Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. *Invertebrate Systematics* 17: 185-259.
- PRENDINI, L., VOLSCHENK, E. S., MAALIKI, S. & GROMOV, A. V. 2006. A 'living fossil' from Central Asia: the morphology of *Pseudochactias ovchinnikovi* Gromov, 1998 (Scorpiones: Pseudochactidae), with comments on its phylogenetic position. *Zoologischer Anzeiger* 245: 211-248.
- PRICE, O., WOINARSKI, J. C. Z., LIDDLE, D. L. & RUSSELL-SMITH, J. 1995. Patterns of species composition and reserve design for a fragmented estate: monsoon rainforests in the Northern Territory, Australia. *Biological Conservation* 74: 9-19.
- REICHERT, H. & BOYAN, G. 1997. Building a brain: development insights in insects. *Trends in Neurosciences* 20: 258-264.
- RUSSELL-SMITH, J. 1991. Classification, species richness, and environmental relations of monsoon rainforest vegetation in the Northern Territory, Australia. *Journal of Vegetation Science* 2: 259-278.
- RUSSELL-SMITH, J. & BOWMAN, D. M. J. S. 1992. Conservation of monsoon rainforest isolates in the Northern Territory, Australia. *Biological Conservation* 50: 51-63.
- RUSSELL-SMITH, J., MACKENZIE, N. L. & WOINARSKI, J. C. Z. 1992. Conserving vulnerable habitat in northern and northwestern Australia: the rainforest archipelago (pp. 63-68). In: MOFFAT, I. & WEBB, A. (eds). *Conservation and development issues in north Australia. North Australia Research Unit, Darwin*, 277 pp.
- SHIVASHANKAR, T. 1992. The importance of burrowing for the scorpion *Heterometrus fulvipes* Koch (Arachnida). *Journal of Soil Biology and Ecology* 12: 134-138.
- SHIVASHANKAR, T. 1994. Advanced sub social behaviour in the scorpion *Heterometrus fulvipes* Brunner (Arachnida). *Journal of Biosciences* 19(1): 81-90.
- SHORTHOUSE, D. J. 1971. Studies on the biology and energetics of the scorpion *Urodacus yaschenkoi* (Birula, 1904). *Ph.D. thesis, Australian National University, Canberra*, 163 pp.

- SHORTHOUSE, D. J. & MARPLES, T. G. 1980. Observations on the burrow and associated behaviour of the arid-zone scorpion *Urodacus yaschenkoi* (Birula). *Australian Journal of Zoology* 28: 581-590.
- SIMON, E. 1880. Etudes arachnologiques. 12ème mémoire. XVIII. Descriptions de genres et espèces de l'ordre des scorpions. *Annales de la Société Entomologiques de France* (5) 10: 377-398.
- SNELLING, A. A. 1992. Alligator Rivers Region Analogue Project, Final Report. Volume 2. Geologic setting. *Australian Nuclear Science and Technology Organisation (ANSTO), Sydney*, 118 pp.
- STACHEL, S. J., STOCKWELL, S. A. & VAN VRANKEN, D. L. 1999. The fluorescence of scorpions and cataractogenesis. *Chemistry & Biology* 6: 531-539.
- STAHNKE, H. L. 1970. Scorpion nomenclature and mensuration. *Entomological News* 81: 297-316.
- STAHNKE, H. L. 1972. UV light, a useful field tool. *Bioscience* 22: 604-607.
- STOCKWELL, S. A. 1989. Revision of the phylogeny and higher classification of scorpions (Chelicerata). *Ph.D. thesis, University of California, Berkeley*, 413 pp.
- SUNDEVAL, C. J. 1833. Conspectus Arachnidum. *Sveno Hardin et Erico T. Hammergren, Vermlandis, London-Göteborg*, 39 pp.
- THORELL, T. 1876. On the classification of scorpions. *Annals and Magazine of Natural History* 4(17): 1-15.
- TILAK, R. 1970. On an interesting observation on the living habit of *Hormurus nigripes* Pocock (Ischnuridae: Arachnida). *Science and Culture* 36: 174-176.
- TOMAREV, S. I., CALLAERTS, P., KOS, L., ZINOVIEVA, R., HALDER, G., GEHRING, W. & PIATIGORSKY, J. 1997. Squid Pax-6 and eye development. *Proceedings of the National Academy of Sciences, USA* 94: 2421-2426.
- VACHON, M. 1956. Sur des nouveaux caractères familiaux et génériques chez les scorpions (pp. 471-474). In: *Proceedings of the XIV International Congress of Zoology, Copenhagen, 5-12 August 1953. Danish Science Press, Copenhagen*, 567 pp.
- VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle (Paris)* (Ser. 2) 35: 161-166.
- VACHON, M. 1974. Etude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle (Paris)* (Ser. 3) 140: 857-958.
- VIGNOLI, V. & PRENDINI, L. 2008. A new species of *Akentrobuthus* Lamoral, 1976 (Scorpiones: Buthidae) from the Republic of Benin (Western Africa). *Journal of Afrotropical Zoology* 4: 61-70.
- VIGNOLI, V. & PRENDINI, L. 2009. Systematic revision of the troglomorphic North American scorpion family Typhlochactidae (Scorpiones: Chactoidea). *Bulletin of the American Museum of Natural History* 326: 1-94.
- VOLSCHENK, E. S. 2002. Systematic revision of the scorpion genera in the family Buthidae. *Ph.D. thesis, Curtin University of Technology*, 224 pp.
- VOLSCHENK, E. S. 2005. A new technique for examining surface morphosculpture of scorpions. *Journal of Arachnology* 33: 820-825.
- VOLSCHENK, E. S., LOCKET, N. A. & HARVEY, M. S. 2001. First record of a troglomorphic ischnurid scorpion from Australasia (Scorpiones: Ischnuridae) (pp. 161-170). In: FET, V. & SELDEN, P. A. (eds). *Scorpions 2001. In memoriam Gary A. Polis. British Arachnological Society, Burnham Beeches, Bucks*, 404 pp.
- WERNER, F. 1939. Ueber einige Scorpione aus dem Museum Alexander Koenig. *Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand (Riga)* 5: 361-362.
- WHITE, C. R. 2001. The energetics of burrow excavation by the inland robust scorpion, *Urodacus yaschenkoi* (Birula, 1903). *Australian Journal of Zoology* 49: 663-674.

- WHITING, M. F., BRADLER, S. & MAXWELL, T. 2003. Loss and recovery of wings in stick insects. *Nature* 421: 264-267.
- WILKINSON, G. S. & DODSON, G. N. 1997. Function and evolution of antlers and eye stalks in flies. (pp. 310-328). *In*: CHOE, J. C. & CRESPI, B. J. (eds). The evolution of mating systems in insects and arachnids. *Cambridge University Press, Cambridge*, 400 pp.
- WILLIAMS, S. C. 1966. Burrowing activities of the scorpion *Anuroctonus phaeodactylus* (Wood) (Scorpionida: Vejovidae). *Proceedings of the California Academy of Sciences* 34: 419-428.
- WYRWOLL, K.-H. 1992. Alligator Rivers Region Analogue Project, Final Report. Volume 3. Geomorphology and palaeoclimatic history. *Australian Nuclear Science and Technology Organisation (ANSTO), Sydney*, 93 pp.
- WITHNALL, I. W., DRAPER, J. J., MACKENZIE, D. E., KNUSTON, J., BLEWETT, R. S., HUTTON, L. J., BULTITUDE, R. J., WELLMAN, P., MACCONACHIE, B. A., BAIN, J. H. C., DONCHAK, P. J. T., LANG, S. C., DOMALGA, J., SYMONDS, P. A. & RIENKS, I. P. 1997. Chapter 14. Review of geological provinces and basins of north Queensland (pp. 449-527). *In*: BAIN, J. H. C. & DRAPER, J. J. (eds). North Queensland geology. *Australian Geological Survey Organisation Bulletin 240 / Queensland Department of Mines and Energy Queensland Geology* 9, 600 pp.